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Cover: *Calymene frontosa* Lindström, from Visby Beds (Silurian) of Gotland, Sweden.
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BRACHIOPOD FOOD AND FEEDING PROCESSES

by H. M. STEELE-PETROVIĆ

Abstract. By considering the available relevant data on morphology, physiology, histology, and biochemistry of the lophophore and digestive tract of brachiopods, and by filling in gaps in the knowledge with analogies drawn from filter-feeding bivalves, a relatively detailed account of feeding processes in brachiopods is presented. It is shown that, except in the expulsion of wastes, similar feeding processes appear to occur in both the inarticulates and articulates. The articulate method of expelling faeces through the mouth has little disadvantage over the inarticulate method of expulsion through the anus. Direct evidence shows that brachiopods are able to assimilate dissolved substances; indirect evidence suggests that bacteria and colloids are utilized, that organic detritus and some algae are important food sources, and that animal forms of life are not important foods for brachiopods. There is no reason to suggest that the food categories of fossil brachiopods differed from those of extant forms. Suggestions are made on how to obtain more information on the food and feeding processes in brachiopods.

The structure of fossil communities cannot be understood without knowing how the animals that lived together in these communities interacted. One of the major regions of potential interaction is competition for food. Since brachiopods were a dominant element in Palaeozoic communities of Ordovician age and younger, knowledge of the food and feeding methods of brachiopods is necessary to understand trophic relationships in the early invertebrate communities, and changes in these relationships with time. Although there is no direct evidence on the food of brachiopods in the past, they are a conservative group of animals, and one would expect the food and feeding processes of Recent species to be similar to those of fossil forms. The food of articulate brachiopods has been a subject of interest in recent palaeontological literature; information has been presented based on examination of gut contents (McCammon 1969; Levinton and Suchanek 1972; Suchanek and Levinton 1974) and on evidence for uptake of dissolved substances (McCammon 1969; McCammon and Reynolds 1972). However, these approaches do not treat all aspects of brachiopod food, and therefore do not lead to a comprehensive interpretation of what the animals in general feed on.

To obtain a broader knowledge of brachiopod food it is necessary to understand how particles are trapped, ingested, and digested, and how waste material is expelled; thus it is essential to have information on morphology, histology, physiology, and biochemistry of the trapping and digestive organs. Sufficient relevant information has been published on these aspects of the biology of brachiopods to enable much reconstruction of the feeding processes, although major gaps in the knowledge remain. However, there are certain similarities between digestive tracts of brachiopods and those of filter-feeding bivalves; and digestion in bivalves is much better understood than that in brachiopods. Therefore information from bivalves on processes that appear to have analogues in brachiopods can be used to fill some gaps in the brachiopod reconstruction. Similarities between inarticulates, articulates,

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and bivalves have been used to set up a general model here for feeding processes in brachiopods. After this model was formulated, Professor Gareth Owen kindly sent me his unpublished information on the digestive tracts of the articulates *Tegulorhynchia* and *Terebratella*, which provides the first evidence on the functioning of the digestive diverticula in brachiopods. That these data demonstrate the essential similarity between the action of the digestive diverticula in brachiopods and in bivalves is a confirmation of an essential aspect of my model; this increases the probability that interpretations of other aspects of brachiopod feeding based on comparisons with bivalves are also valid.

FUNCTIONS OF THE TRAPPING ORGANS

The lophophore, the trapping organ of brachiopods, consists of two arms (brachidia) looped symmetrically one on each side of the mouth. Each brachidium consists of a cartilaginous brachial axis that bears along its entire length both a ciliated food-groove bounded by a muscular lip, and two parallel rows of long, slender flexible filaments perpendicular to the axis. Cilia occur around the brachial axis, on the sides and fronts of the filaments, and on the backs of inarticulate filaments; but they are usually rare or absent on the backs of articulate filaments (see Chuang (1956) and Rudwick (1970, pp. 117ff.) for descriptions of brachiopod lophophores). The structure of the lophophore is similar in all extant families of brachiopods, and fossil evidence shows that it has not changed, at least in one group of terebratulids, since the Cretaceous (Rudwick 1970, p. 120). Since the preservable parts of the different brachiopod orders have remained similar throughout the evolution of these groups, it is assumed that the basic structure of the lophophore and alimentary tract has not changed, and that brachiopods have always fed in the same manner.

When a brachiopod is feeding, the lateral cilia on the filaments beat in a metachronal wave from the frontal to abfrontal surface of the filaments, and produce an inhalant water current that passes between the filaments from the frontal to abfrontal side (Atkins 1958, 1960). Some of the material that is suspended in the incoming water is collected by the lophophore, but a large proportion is carried through it and out with the exhalant current (Rudwick 1962; Steele-Petrović 1975). Bullivant (1968) has suggested that sharp deflection of the water around the tentacles causes certain suspended particles to be thrown against the frontal surfaces of the tentacles, and that selection of these particles depends on their velocity, density and size, radius of curvature of the deflection, and viscosity of the sea-water. He introduced the term ‘impingement-feeders’ for animals that collect potential food material in this manner. Once particles have impinged on the frontal surfaces of brachiopod filaments, no sorting appears to take place (Rudwick 1970, p. 121). The material is carried indiscriminately to the base of the filaments in a local current created by the frontal cilia (Chuang 1956), and then into the ciliated food-groove which leads directly to the mouth. As Chuang noted for *Lingula*, other suspended particles may contact the outer surface of the brachial lip; the beating of cilia that occur there subsequently carries this material over the lip and into the food-groove.

It is generally assumed that brachiopods continuously feed when the valves are open and an inhalant current is being produced. However, trapping and ingestion of particles probably ceases when the stomach becomes full; for (as is discussed later) ingested particles, regardless of food value, all appear to be retained in the stomach while digestion takes place. A brachiopod can prevent particles from reaching the mouth by stopping the frontal cilia and closing the food-groove; this should not prevent lateral cilia from maintaining an inhalant current for continued oxygen supply. Trapping and ingestion probably resume after digestion of food and expulsion of undigested material from the stomach have occurred. If the feeding system becomes overloaded with trapped material, the only recourse is wholesale rejection as described by Chuang (1956), Atkins (1958, 1960), and Rudwick (1962, 1970). The animal ceases feeding by closing the lip of the food-groove and by stopping the beat of the lateral cilia; mucus secreted by the filaments engulfs the particles and the frontal cilia reverse direction of beat, or in the case of *Lingula*, where adjacent rows of frontal cilia appear to beat permanently in opposite directions (Chuang 1956), those beating towards the tips of the filaments beat more strongly. The mucus-bound particles are thus carried to the tips of the filaments and on to the mantle surface from where they are rejected as pseudofaeces. In some brachiopods reversal of the lateral cilia aids in the rejection process by producing a current that flows in the opposite direction to the feeding current. Chuang (1956) has shown that *Lingula* can get rid of single large particles while continuing to feed. Only Atkins (1958) has observed a simultaneous acceptance of some particles and rejection of others by the lophophore, and she stated that this action was seen only in a few specimens, although in several different species. She observed that occasionally those particles that were trapped by the frontal filaments were transported to the tips of the filaments and rejected from the shell, while those trapped by the abfrontal filaments were transported in the opposite direction to the food-groove. There is no information on the details of water-flow around the filaments, and on whether particles hitting the two sets of filaments differ. However, it seems unlikely that the action described by Atkins is used as a sorting mechanism, as she suggested, for it appears to occur too rarely.

The role played by mucus in the transportation of accepted particles along the filaments to the food-groove is probably minor; Orton (1914) claimed that a mucus sheet aids in the capture and retention of food particles, and that these particles when bound in mucus are easily transported along the filaments (he insinuated towards the mouth) by frontal cilia. However, Chuang (1956) observed that particles are water-borne on the frontal surfaces of the filaments of *Lingula*, and that mucus is unimportant except under unfavourable conditions such as abnormally high turbidity. Rudwick (1962) saw that mucus was produced only when a rejection mechanism was working, and then a sheet of mucus entangled the unwanted particles. R. G. B. Reid has suggested to me that minute, indiscernible amounts of mucus may impart a stickiness to particles that may be important. However, one can conclude that Orton was describing a rejection mechanism. He did not mention what his animals were fed, but Rudwick (1962) found that rejection took place when brachiopods were fed even dilute suspensions of carmine, graphite, carborundum, starch, or milk; materials that are usually used in the study of ciliary currents of suspension-feeding animals. By contrast with transport along the filaments, potential food particles that contact the outer surface of the brachial lip may or may not be entangled in discernible amounts of mucus before they are carried into the food-groove (Chuang 1956); but all particles, once they have reached the ciliated food-groove, are bound into a string of mucus for transport to the mouth (Richards 1952; Chuang 1956).

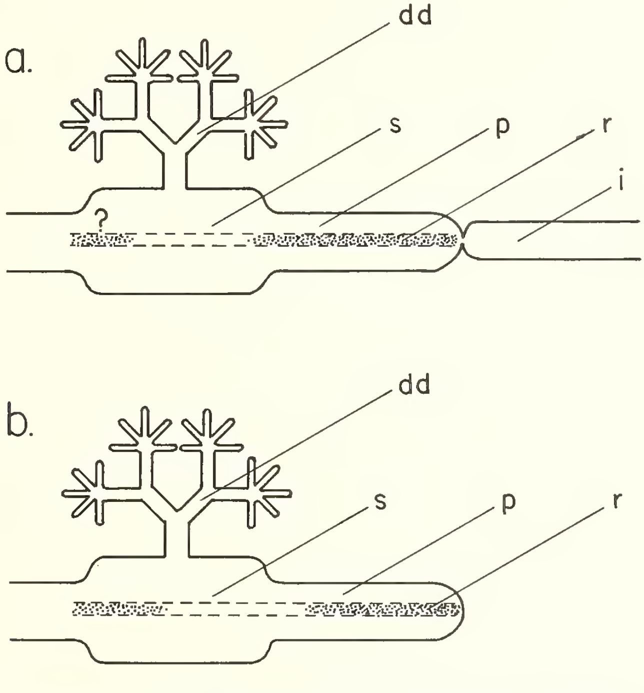
Thus it seems that brachiopods are non-selective feeders, and either accept or reject all material that is collected from the inhalant current. Because of their open filamental structure they are able to trap only a small proportion of particles that are suspended in the incoming water. Most of these particles are probably non-motile. As suggested by Bullivant (1968), rapidly moving protistans can probably readily escape from the exposed frontal edges of the filaments. If mucus were present it would aid in holding the motile forms, but not much mucus is secreted by the filaments during the normal feeding process. However, mucus is secreted normally by the outer surface of the brachial lip and by the ciliated food-groove; and swimming protistans that make direct contact with these areas would become entangled in mucus and trapped. The muscular lip probably also aids in retaining any motile forms that enter the food-groove. Polychaete fan worms, which are also impingement-feeders, are able to hold swimming algae at only one-tenth the efficiency with which they hold inert particles (Dales 1957).

FUNCTIONS OF THE DIGESTIVE ORGANS

Information on the alimentary tracts of brachiopods is available for the inarticulates *Lingula*, *Crania*, and *Discinisca* (Blochmann 1892, 1900; Chuang 1959, 1960), and the articulates *Magellania* (*Waldheimia*) (Joubin 1892), *Pumilus* and *Macandrevia* (Atkins 1958), and *Tegulorhynchia* and *Terebratella* (kindly supplied by G. R. G. Owen). The alimentary tract in both inarticulates and articulates includes pharynx, oesophagus, so-called anterior stomach in the inarticulates or stomach in the articulates (here called stomach for both groups), digestive diverticula, and so-called posterior stomach in the inarticulates or intestine in the articulates (here called pyloris for both groups). The articulate gut is blind and terminates at the end of the pyloris, whereas in the inarticulates it is continuous and has an intestine connected by an anus to the outside (see text-fig. 1A, B). In general the number of digestive diverticula is constant within a species but varies between species (see Blochmann 1892, 1900; Hyman 1959, p. 552; Chuang 1959, 1960); each diverticulum typically consists of bunches of blind acini which are connected to the stomach chamber by a series of branching ducts.

The only detailed description of the functions of a brachiopod gut has been given by Chuang (1959) for *Lingula unguis*. He noted that when this species is feeding, the mucus-bound string containing trapped food particles is carried by ciliary currents through the mouth and into the pharynx in little shreds. He did not indicate how the shredding process takes place. Chuang also described the stomach contents of *L. unguis* as 'fluid and particles'; this description implies that after ingestion, potential food particles are released from their binding mucus in order for digestion to occur. Yonge (1935) studied a number of species belonging to several phyla that transport trapped particles in mucus. He found in all cases that the stomach pH approximates the value at which the mucus in question is least viscous, and therefore least able to hold its trapped particles. Although no brachiopods were studied by Yonge, it seems reasonable to assume that pH of the lingulid stomach is also responsible for breaking down mucus and releasing food.

The walls of the alimentary tract in both groups of brachiopods are muscular (see Joubin 1892; Blochmann 1892, 1900; Chuang 1959, 1960). Both Joubin (1892) and Chuang (1959, 1960) noted that the guts are lined throughout with columnar epithelium which is ciliated everywhere except for the acini of the digestive diverticula. Ciliary currents in the alimentary tract are generally directed in a posterior direction (Atkins 1958; Chuang 1959), although a strong anteriorly flowing current occurs along the mid-ventral line in the articulate stomach (Atkins 1958).



TEXT-FIG. 1. *a*, schematic diagram of inarticulate gut. Based on information in Chuang (1959). *b*, schematic diagram of articulate gut. Based on information from Atkins in Morton (1960). dd, digestive diverticula; i, intestine; p, pyloris; r, mucus-bound rod; s, stomach.

According to Chuang (1959) the posteriorly directed currents in *Lingula* serve only to keep the gut contents agitated and mixed, and muscular action of the gut walls is responsible for through-going movement of the contents. Also, in both inarticulates and articulates, a clockwise rotation (when viewed from the anterior end) is produced by the beating of cilia in both the anterior region of the stomach and posterior region of the pyloris (Atkins 1958; Chuang 1959; Owen, written communication); rotation is stronger and faster in the pyloris (Chuang 1959; Morton 1960).

When *L. unguis* is actively feeding and digesting, ciliary rotation in the stomach ceases or greatly decreases, and the digestive diverticula undergo muscular pulsations (Chuang 1959). These pulsations appear to occur universally among brachiopods. In *L. unguis* each diverticulum in turn relaxes usually in order of position, anteriorly to posteriorly, causing the branching ducts and acini to expand and suck in fluid and particles from the stomach. No sorting or rejection of the ingested material takes place in the stomach of either group (Chuang 1959; Owen, written communication), and all ingested particles stand a chance of being sucked into the digestive diverticula. Relaxation is followed by a contraction which forces the fluid and particles back into the stomach. Chuang (1959) noted that the number of cycles of relaxation and contraction varied from one to twelve (on the average about four) per minute depending on size of the individual and phase in the feeding cycle; he stated that at the height of feeding activity in one specimen, the pulsation rate was twelve per minute (an unusually fast rate), slowing down to three per minute one and a half hours later when most of the particles had left the stomach; time for relaxation was usually about ten times that for contraction. Owen observed (written communication) that particles visible to him in the acini of *Tegulorhynchia* and *Terebratella* appeared to move toward the stomach during contraction but remained stationary during relaxation; he suggested that relaxation of the acini may have been so slow that only the fluid and particles too fine to be visible under the binocular were drawn into the acini. Judging from Chuang's descriptions of changes in rate of pulsation within a single specimen, it appears that Owen's observations may be typical of a specimen at a particular phase of its feeding activity. Owen also noted that cilia occurring where the ducts of the digestive diverticula meet the stomach all beat into the stomach. Chuang (1959) observed that cilia in the branching ducts beat toward the stomach and are responsible for a strong outer current along the walls and a weaker current going toward the acini in the middle of the ducts. Particles in the ducts get passed from one ciliary current to the other, suggesting to Chuang that the function of the currents is to keep the contents of the digestive diverticula mixed.

According to Chuang (1959) most intracellular digestion in brachiopods appears to occur in the acini of the digestive diverticula. These acini in *L. unguis* are tubular to globular sacs (Chuang 1959) and in *Tegulorhynchia* and *Terebratella* are long, finger-like and unbranched (Owen, written communication). Both Joubin (1892) and Chuang (1959, 1960) noted that, unlike the epithelial lining of the rest of the digestive tract, that of the acini is unciliated. Blochmann (1892), however, reported that ciliated epithelium lines the digestive diverticula of *Crania anomala*. However, Blochmann found it difficult to section the digestive diverticula, and erroneously thought that the epithelial structure in both acini and ducts is the same, but differs from that in the rest of the gut. One therefore suspects that Blochmann was actually describing epithelium of the ducts rather than that of the acini of the digestive diverticula. Chuang (1959, 1960) has shown that in both *Lingula* and *Crania* the cells lining the acini, unlike those of the rest of the gut, bulge into the lumen at various heights and form an uneven surface. Two kinds of cells occur in the digestive diverticula of brachiopods, as noted by Joubin (1892) in *Magellania* and by Owen (written communication) in *Tegulorhynchia* and *Terebratella*.

Yonge (1926*a*, *b*) showed that bulges on the diverticular cells of filter-feeding bivalves are pseudopodial extensions which phagocytose fine particles of solid matter and absorb soluble material; more recent evidence shows that these digestive cells also take in particulate matter by pinocytosis (Owen 1970). The same is true in brachiopods. Professor Owen reports on *Tegulorhynchia* and *Terebratella*: 'I have clear evidence of the ability of the large digestive cells to ingest particulate material both by phagocytosis and pinocytosis and it is clear from a preliminary examination under the microscope that these digestive cells, as in bivalves, possess a well-developed lysosomal system which serves to process the ingested material.'

Apart from the digestive cells, epithelial cells of another type, basiphil cells, also occur in diverticular tubules of all bivalves (Sumner 1966; McQuiston 1969; Owen 1970, 1974; Pal 1971). In filter-feeding bivalves basiphil cells are present in the crypts of these tubules; the basiphil cells may be flagellated, or if not flagellated, another type of flagellated cell may be associated with them (Owen 1974). Similar cells were noted by Professor Owen in the digestive diverticula of the articulate brachiopods *Tegulorhynchia* and *Terebratella*; he writes: 'The tubules [i.e. acini] possess flagella and it is almost certain that, as in bivalves, these are borne by the dark staining cells of the crypts.' Although Joubin's (1892) descriptions of the two types of cells that occur in the digestive diverticula of *Magellania* are not very detailed in comparison to the much more recent descriptions for bivalves, his Type 2 cells 'qui contiennent toutes, vers leur tiers supérieur, un amas de grosses granulations', probably correspond to vacuolated (digestive) cells found in bivalves, and his Type 3 cells, which differ from Type 2 'par le diametre plus petit des granulations . . . répandu[e]s dans toute l'étendue de la cellule', may correspond to the basiphil cells of bivalves with their finely granular cytoplasm but no vacuoles (cf. Sumner 1966). Recent evidence suggests that the basiphil cell in bivalves is secretory (Sumner 1966; McQuiston 1969; Owen 1970), although this interpretation has been disputed by Pal (1971). There is no information on the function of basiphil-like cells in brachiopods, but it probably corresponds to that of basiphil cells in bivalves.

Chuang (1959, 1960) noted that epithelial bulges in the inarticulate acini break away and form blobs of various sizes in the lumen of the digestive diverticula. Similar discharge that occurs in filter-feeding bivalves is now attributed to cyclic disintegration of their absorptive cells following completion of intracellular digestion (Purchon 1971; Morton 1973). There are no data on possible cyclicity in brachiopods. Indigestible particles that brachiopods take into the cells of the digestive diverticula are probably expelled in these blobs, as Owen (1955) described for bivalves.

Brachiopods all appear to have a ciliated epithelial groove which begins in the stomach chamber and extends to the posterior end of the pyloris (Joubin 1892; Blochmann 1900; Atkins 1958; Chuang 1959, 1960). In *Lingula*, the only genus for which there is detailed information, the epithelial groove arises in the vicinity of the digestive diverticulum that is situated most posteriorly; according to Blochmann (1900) it begins just behind the entrance to the posterior digestive diverticulum in *L. anatina*; whereas Chuang (1959) noted that in *L. unguis* it starts in the anterior ducts of this same posterior diverticulum. In *Lingula*, particles that are rejected by the digestive diverticula are bound into a mucous rope in the ciliated epithelial groove and transported within it by ciliary currents to the pyloris (Chuang 1959). The rejected material, similar to that in the intestinal groove of bivalves, is isolated from the region of active feeding in the stomach, and therefore should not contaminate those particles that are being actively passed back and forth between the stomach and digestive diverticula. Chuang (1959) reported that in *L. unguis* the mucus-bound rope may leave the groove at the posterior end of the pyloris and rotate axially in a manner somewhat reminiscent of the crystalline style of bivalves. Atkins (1958) noted that in the articulates the rotating string of mucus-bound particles that is found in the pyloris may stretch into the stomach and come under the influence of the anterior rotating region, thus being rotated at both ends. Atkins called the rotating string a protostyle. However, as in *Lingula*, ciliary rotation probably ceases in the articulate stomach during muscular pulsations of the digestive diverticula. Thus it is probable that growth of the rotating string anteriorly into the stomach only occurs after active digestion has ceased. But rotating mucus-bound matter in the anterior rotating region need not be only the result of growth of the protostyle anteriorly; both Atkins (1958) and Morton (1960) suggested that after digestion is complete in the articulates, unused material is expelled from the digestive diverticula into the stomach where it is bound by mucus and rolled into a bolus by the anterior rotating area; and products of disintegration of the digestive diverticula might periodically be discharged *en masse* into the stomach, if feeding processes in brachiopods are cyclic.

The processes that take place in the brachiopod stomach include both the disintegration of mucus and the formation of a mucus-bound anterior cord. Goblet-shaped mucus cells generally occur among epithelial cells of the digestive tract (Joubin 1892; Blochmann 1892, 1900; Chuang 1959, 1960). However, stomach conditions that favoured the breakdown of mucus that bound the incoming food particles would not favour the formation of a faecal cord that is bound by the same kind of mucus. If the incoming mucus breaks down chemically because of the pH of the stomach, either there must be a change in the stomach pH after digestion, or mucus that is produced in the stomach must differ from that formed in the food-groove, and have its lowest viscosity at a different pH. Stomach pH in bivalves decreases when the digestive diverticula break down and discharge their relatively acidic products into the stomach (Purchon 1971; Morton 1973); the same may occur in brachiopods.

There is no record of an anterior mucus-bound string being formed in the rotating area of the inarticulate stomach. However, it seems likely that at the end of the muscular contractions of the digestive diverticula, undigested material would be expelled into the stomach, as has been postulated for the articulates; large numbers of globules from the digestive diverticula might also be shed into the stomach; but whether this material is then passed into the pyloris bound in mucus, or unbound, is unknown. If it is passed unbound, the inarticulates would not require changes in stomach conditions that would permit breakdown of mucus at one time and its formation at another. If mucus disintegrates in one part of the inarticulate gut and is produced in another part, it is possible that pH differs in different parts of the gut. Such is the case in some other invertebrates (Yonge 1935). The only information on pH of the inarticulate gut indicates that it is the same throughout (Chuang 1959). However, it is possible that a difference in pH is present only at certain times during the feeding process, and that none of the animals tested by Chuang were at the critical feeding stage.

In the articulates the part of the gut where posterior rotation occurs is usually referred to as the 'intestine', and according to Atkins (1958), it may be considered embryologically and functionally to be intestine. In the inarticulates this rotating region is called 'posterior stomach' by Chuang (1959, 1960). The area is morphologically, physiologically, and histologically similar in both groups of brachiopods, and, according to Morton (1960), similar in function to the pyloris of other impingement-feeders. Thus it seems best to call the posterior rotating area of all brachiopods the 'pyloris' (as Morton appeared inclined to do), instead of using different names for each group. The brachiopod pyloris also resembles the style sac of molluscs (Atkins 1958; Chuang 1959).

In the inarticulate gut a sphincter occurs at the posterior end of the pyloris, and by relaxing at regular intervals it enables waste material to empty by peristalsis into the intestine (Chuang 1959). An anal sphincter is also present; its relaxation permits intestinal contents to be expelled, also by peristalsis. Because of the blind gut in the articulates, their faecal matter is expelled through the mouth by antiperistalsis (Richards 1952; Atkins 1958); their stomach cord must be eliminated with each defecation, while that in the pyloris is possibly expelled only occasionally. Rejected material is packed into pellets by the intestine in the inarticulates, and, according to Morton (1960), probably at the oesophagal end of the stomach in the articulates. In both cases pellets are expelled into the mantle cavity. Rudwick (1962) described for the articulates how a faecal pellet, after it leaves the mouth, is transported by the filaments and by the cilia of the mantle surface to the postero-lateral corner of the shell, whence it is expelled by rapid closure of the valves. Likewise, inarticulates eject pellets by sudden snapping of the valves (Rudwick 1970, p. 123), probably also each time one is produced, for if faecal matter is not immediately expelled from the valves, fouling of the mantle cavity is possible even though the pellets are bound in mucus.

Both types of brachiopods are functionally suited for ingestion and digestion of particulate material, and expulsion of particulate wastes. The articulate gut is not reduced so that its prime food must be dissolved and colloidal material as suggested by McCammon (1969), nor, as is apparent from a later discussion of enzymes, is the pyloris reduced to being able to absorb nothing at all, as suggested by McCammon and Reynolds (1972).

The only gross difference between the alimentary tracts of the two groups of brachiopods is that in the articulates the gut is blind and ends with the pyloris, and in the inarticulates it is through-going and ends in an anus. In other respects the digestive tracts are morphologically and histologically similar. Although information on digestive processes in brachiopods is relatively detailed only for *L. unguis*, evidence for other species, when present, always either corroborates or complements that from *L. unguis* (except when concerning expulsion). It is therefore suggested that, except in the expulsion of waste, very similar physiological processes occur in the alimentary tracts of both kinds of brachiopods.

RELATIVE FEEDING EFFICIENCIES OF THE INARTICULATES AND ARTICULATES

The feeding process in the articulates has not been considered as efficient as that in the inarticulates, because with each defecation an articulate must cease feeding and expel its stomach contents. However, there is evidence to suggest that the articulate method of expelling faeces through the mouth has little disadvantage over the inarticulate method of expulsion through the anus. Ingestion should cease as soon as the brachiopod stomach is full, and it should not resume until after digestion has occurred and the stomach has emptied. Therefore intake of food particles should have ceased in articulates some time before expulsion of wastes through the mouth. But even if food intake is continuous, ingestion must cease when the valves close, and both kinds of brachiopods rid the mantle cavity of faecal pellets by sudden snapping of the valves; therefore, the articulates are unlikely to have a disadvantage unless they spend appreciably more time in expelling wastes than the inarticulates. The only information available on rate of expulsion indicates that the articulates eliminate only one or two faecal pellets per hour and close their valves for just a few minutes each time (see Savage 1972). Since the articulates appear to spend only a small percentage of their time expelling wastes, they are unlikely to lose significantly more potential feeding time than the inarticulates because of this function. Digestion in both groups of animals probably ceases during defecation; it is obvious that it must in the articulates; and although it is not so obvious in the inarticulates, Chuang (1959) noted that the pulsation rate of the digestive diverticula in *Lingula* is substantially reduced when gut contents pass from the pyloris into the intestine. The relative efficiencies of inarticulates and articulates appear to be comparable.

BRACHIOPOD FOOD

Few controlled experiments have been done in order to determine what brachiopods can ingest and digest. No field studies appear to have shown what they live on under natural conditions, and, as Cowen (1971) has indicated, the food of any particular specimen probably depends on habitat, latitude, depth, and season. As described above, it appears that all brachiopods trap, ingest, and digest food material in a similar manner, and thus all brachiopods are grouped in this section.

Ingestion. Most information on particulate material ingested by brachiopods is from the contents of their alimentary tracts. However, not all material that is trapped may be present in the gut at the time of dissection, for easily digestible material may have been assimilated without leaving a trace. Also small forms, such as bacteria, easily escape detection under a microscope.

The particulate material in brachiopod guts appears to consist primarily of micro-organisms and inert particles in varying proportions. Large percentages of clay particles have been reported from the guts of numerous specimens (McCammon 1969; Levinton and Suchanek 1972; Suchanek and Levinton 1974). Diatoms and dinoflagellates are the micro-organisms most frequently found (Blochmann 1900; Rudwick 1965, p. H205; McCammon 1969; Levinton and Suchanek 1972; Suchanek and Levinton 1974). If, as discussed above, large motile protistans readily escape from brachiopod filaments, non-swimming micro-organisms should be ingested more frequently than swimming forms. However, there is no information on the relative sizes and numbers of swimming and non-swimming forms that have been found in brachiopods. Levinton and Suchanek (1972) gave the names of several diatom genera abundantly found in the guts of the brachiopods they dissected, and all are non-motile. This favours the theory of easy escape of swimming forms, although the genera mentioned by these authors may not be representative of the entire contents of the guts of the specimens they dissected or of brachiopods in general. Blochmann (1900) reported the presence of tests of motile forms such as armoured dinoflagellates, small foraminifera, and bivalve and gastropod larvae; his descriptions imply that the tests were empty, and if that were the case, they were probably empty when ingested (for reasons given later). Owen (written communication) noted that in the stomach contents of the specimens of *Terebratella* he studied, apart from diatoms, there were sponge spicules and sand grains (the latter of rather constant size); and that the compact rod in the pyloris appeared to consist largely of these sand grains embedded in mucus.

Digestion. It is necessary to differentiate here between ingestible and digestible material. Most evidence presented on the particulate food of brachiopods has been based on gut contents. But because all material that is trapped by the lophophore is indiscriminately passed to the mouth and into the gut, both digestible and indigestible material is likely to be taken in in various proportions. Easily digested material may be assimilated relatively quickly so that no trace of it remains at the time of dissection. In view of the similarities with bivalves, it is significant that Ballantine and Morton (1956) found no evidence of minute and naked flagellates in the guts of the bivalve *Lasaea rubra*, only a short time after these protistans had been eaten. Reid (written communication) states that naked micro-organisms are unrecognizable minutes after entering an oyster stomach. Also, as noted above, particulate waste material is not continuously expelled by brachiopods, but accumulates in mucus-bound cords and is retained temporarily in the stomach and pyloris. Therefore, brachiopod gut contents may at times be a better indication of indigestible than of digestible material. In fact McCammon (1969) noted that the material she recovered from brachiopod guts was in most cases compacted into a bolus. Levinton and Suchanek (1972) reported the heavy-walled diatom *Thalassiosira* occurring commonly in gut contents of shallow-water *Terebratalia*; Ballantine and Morton (1956) showed that the bivalve *L. rubra* could only slightly digest this diatom genus, and that most of the cells were passed out in faeces. The degree of assimilation of much material varies with its retention time in the stomach; if a relatively large percentage of ingested matter is easily assimilated, the rate of renewal of stomach contents might be too fast for the more resistant forms to be decomposed; a longer retention time might permit at least partial breakdown of these forms.

In spite of the above limitations some information on brachiopod food can be inferred from gut contents. Prior to McCammon's (1969) study it was assumed that brachiopods feed chiefly on diatoms and dinoflagellates (see Rudwick 1965, p. H205). McCammon noted a large percentage of clay in the guts of the specimens she dissected, and concluded that these animals obtain much of their nourishment from material that is sorbed on the surface of clay particles. This conclusion seems reasonable since most of her animals were collected from deep water where other food is likely to be scarce. McCammon assumed the sorbed material to be organic colloids, and there is evidence to suggest (Verwey 1952) that colloids are a source of nutrition for bivalves. However, Newell (1965) showed that the deposit-feeding bivalve *Macoma balthica* digests bacteria that coat ingested particles of mud and organic debris. Newell suggested that suspension-feeders with fine-grained sediment in the guts may also feed on bacteria. Since bacterial concentrations may be high in the top centimetre of marine mud (Jørgensen 1966, pp. 216, 286), it is possible that McCammon's brachiopods were utilizing such bacteria as well as, or instead of, organic colloids.

Laboratory experiments have shown that brachiopods can assimilate certain dissolved substances. After placing *Terebratalia transversa* into dilute suspensions of radioactive glucose, McCammon and Reynolds (1972) were able to trace the uptake of C^{14} through the surfaces of the lophophore and mantle, and then trace the subsequent transport of nutrient products to muscles and other tissues. The experiment lends support to McCammon's (1969) suggestion that several species of articulate brachiopods that survived in the laboratory for up to 2 years lived on dissolved nutrients, the only food that was supplied. McCammon (1973) has also suggested on the basis of histological similarities between the lophophores of *T. transversa* and *Magellania venosa* that *M. venosa* is able to absorb dissolved material in the same way. However, uptake of dissolved nutrients, including uptake through the body wall, is common in invertebrates that feed primarily on other things (Stephens 1968; Southward and Southward 1972*a*, *b*), and it may occur in many brachiopods. But, as these authors and others have stressed, the ability of a species to assimilate dissolved compounds is not an indication that the animal depends heavily on this type of food, but rather that it has the ability to use dissolved material to augment the rest of its diet. Another potential food of brachiopods may be the loosely compacted organic-mineral aggregates found by Rhoads (1973) and Johnson (1974) to occur commonly at the sediment-water interface in shelf deposits. These aggregates consist of an amorphous matrix containing mineral particles that range in size from a few to several hundred microns in diameter. They appear to be faecal material, and should be high in bacteria (Rhoads 1973; Johnson 1974).

To determine the methods used by *Lingula unguis* in assimilating food particles, Chuang (1959) fed starved specimens with carmine particles in one experiment, and with an emulsion of olive oil in a second experiment. The animals were killed one day after feeding began, and microscopic examination of both fixed and fresh specimens revealed globules of ingested material in most regions of the digestive tract: in both epithelial and mesothelial cells throughout the gut, and in wandering phagocytes that were found among the intestinal contents or among the epithelial cells of the stomach, pyloris, and intestine. (Wandering phagocytes (amoebocytes) are found in both groups of brachiopods (Joubin 1892; Chuang 1959, 1960); in *Lingula* they are reported by Chuang (1959) to occur both in the lumen and among epithelial cells of the gut; Joubin (1892) discussed their presence among the epithelial cells in *Magellania*, but did not report them in the lumen of its digestive tract.)

In the epithelial cells of the acini, Chuang (1959) found carmine particles up to

1·2 μm in diameter and oil droplets 0·8–0·9 μm in diameter. Smaller particles of both substances were present in mesothelial cells of the digestive diverticula. The epithelium and mesothelium of the rest of the gut also contained both carmine and oil: carmine particles were about 0·4 μm in diameter in epithelial cells of the stomach and pyloris, and up to 1·2 μm in the intestine; oil droplets were as large as 5 μm throughout. Wandering phagocytes in the lumen of the intestine held carmine particles that reached 2 μm diameter; those in the epithelial cells of the stomach, pyloris, and intestine contained oil droplets as large as 2 μm. Oil droplets were also found in phagocytes that occurred in the intestinal contents. Chuang (1959) observed that olive oil accumulated in *L. unguis* largely in the epithelium of the acini of the digestive diverticula. He concluded that the epithelial cells of the acini are the chief sites of ingestion. Phagocytes may pick up food from the epithelium and carry it throughout the body as Joubin (1892) noted in *M. venosa*, and as Yonge (1926*a*) similarly noted in the bivalve *Ostrea edulis*. Chuang (1959) observed that wandering phagocytes in the lumen of the gut of *L. unguis* ingested food particles; but he thought that these cells remained too scarce to play an important role in digestion, even though they increased in numbers after an animal had fed. Chuang's experiments showed that particles that had been engulfed by wandering phagocytes were larger than those found in the epithelial cells (oil droplets amalgamated to form larger masses in the mesothelium). On the basis of similar observations in bivalves, Yonge (1926*a*, *b*) and Takatsuki (1934) suggested that the role of free phagocytes is to take in particles that are too large to be ingested by the diverticular cells. Joubin (1892) reported to have observed food particles pass unaided between cells of the stomach epithelium of *M. venosa*; it is difficult to imagine a mechanism of transport, unless the particles were carried by phagocytes, as Yonge (1926*a*) observed in *O. edulis*. However, phagocytic action does not seem to be important in the lumen of the digestive tract of all bivalve species at all times (see George 1952; Ballantine and Morton 1956); the same may be true for brachiopods. Chuang (1959) also suggested that food particles may be ingested by epithelial cells of the gut wall, but since these cells are non-phagocytic it seems improbable that they are able to directly ingest particulate material. Particles found in cells of the gut wall of *L. unguis* can be explained by phagocytic transfer from the lumen through the wall (a possibility not completely rejected by Chuang), or by similar transfer from sites of ingestion in the acini.

It is also necessary to consider the biochemistry of digestion in brachiopods. In digestion, large molecules of food matter undergo hydrolysis in the presence of enzymes (organic catalysts) and are broken down into small molecules. This breakdown may occur intracellularly or extracellularly; if intracellular, the particles are taken into cells by phagocytosis and pinocytosis and there they encounter intracellular enzymes; in extracellular digestion, hydrolysis of food particles is catalysed by enzymes that are in the lumen of the gut (extracellular enzymes), and particles that are too large to be digested intracellularly are reduced in size sufficiently to be phagocytosed or to be absorbed by the gut epithelium. The assimilated material is transferred to other parts of the organism for storage and subsequent uses in metabolic processes. As it is characteristic of enzymes to catalyse one kind of reaction (i.e. reactions involving substrates with identical linkage between the molecules) or often one particular reaction (Baldwin 1967, p. 6), the enzymes, their relative strengths, and where they occur in the digestive system of an animal, give some indication of what the animal can digest and how digestion takes place.

Little information has been published on brachiopod enzymes and their distribution. Chuang's (1959) determinations for *L. unguis* are the only published account of an attempt to determine several enzymes in the digestive system of a single brachiopod species. There is also not much information on the natural occurrences of substrates on which these enzymes act. The available data (Tables 1 and 2) on enzymes indicate that carbohydrate digestion in *Lingula* is dominant both intracellularly and extracellularly. Reserve carbohydrates of chlorophyll-bearing plants (amylose and sucrose) and the digestive product of starch (maltose) appear to be important foods for *Lingula*; as they appear to be for marine invertebrates in general (see Kristensen 1972). It is not clear why lactase is strong in certain regions of the alimentary tract,

TABLE 1. Enzyme occurrences in the digestive tracts of brachiopods.

☐ Lingula unguis ◇ Lingula lingula ○ Coptothyris grayi ● very strong ◕ strong ◑ moderate ◔ weak ∅ absent		STOMACH	STOMACH CONTENTS	DIGESTIVE DIVERTICULA	PYLORIS	INTESTINE	WHOLE DIGESTIVE TRACT	TOTAL ORGANISM
	PROTEASE	⧄[1]	⧄[1]	◳[1]	⧄[1]	⧄[1]		∅[5]
	LIPASE	⧄[1]	⧄[1]	◳[1]	⧄[1]	⧄[1]		
CARBOHYDRASES	AMYLASE	▟[1]	▟[1]	■[1]	▟[1]	▟[1]		
	ALGINASE			∅[2]				
	LAMINARANASE			◔[3]				
	SUCRASE			■[1]		▟[1]		
	INULASE			■[1]		◳[1]		
	RAFFINASE			◳[1]		◳[1]		
	MALTASE			▟[1]		■[1]		
	LACTASE			▟[1]		■[1]		
	METHYLCELLULASE			⬘[4]			◕[6]	
	CHITINASE						∅[6]	
	METHYLCHITINASE						◕[6]	

1. Chuang (1959).
2. Favorov and Vaskovsky (1971).
3. Sova *et al.* (1970).
4. Yokoe and Yasumasu (1964).
5. Kozlovskaya and Vaskovsky (1970).
6. Elyakova (1972).

TABLE 2. Enzymes that are referred to in the text, their substrates, and known occurrences of substrates.

Enzymes	Substrate hydrolysed by enzyme	Natural occurrences of substrates
Amylase	Amylose (starch)	Reserve material of all chlorophyll-containing plants (1).
Laminaranase	Laminaran	Reserve material that is ubiquitous in brown algae (3). Important reserve in diatoms (3). Also found in Chrysophyta and euglenoids (1). Polysaccharides similar to laminaran probably most common polysaccharides in nature; in higher plants (3). Similar polysaccharides appear to be important component of marine particulate material (1).
Maltase	Maltose	Sugar that is liberated by digestion of starch; does not often occur free in nature (2, p. 42).
Sucrase	Sucrose	Reserve substance of all chlorophyll-containing plants (1). Various amounts in green and red algae, traces in brown algae (3). Free sucrose rare in animals (1).
Raffinase	Raffinose	Common in higher plants; doubtful if occurs in algae; has been reported from bacteria (1).
Lactase	Lactose	In milk of mammals; occasionally in pollen of higher plants (1).
Alginase	Alginic acid	Major constituent of cell walls of brown algae (4). Has been found in bacteria grown under artificial conditions (1).
Inulase	?	?
Cellulase	Cellulose	In cell walls of higher plants and algae, except blue-green algae (4). Found in fungi and certain bacteria; rare in animals except tunicates (1).
Methylcellulase	Methylcellulose	Degraded cellulose, water soluble (1).
Chitinase	Chitin	Structural component of several invertebrate phyla, particularly arthropods, molluscs, annelids; found in fungi and diatoms (1). Found in cell walls of some green algae (4). Found in yeasts (2, p. 90). Chitinase and cellulase may be identical for cellulase also hydrolyses chitin (Baldwin 1967, p. 75).
Methylchitinase	Methylchitin	Degraded chitin?
Protease	Protein	Found in all plants and animals; main constituent of animals (2, p. 87). Small quantities in cell walls of algae (4). As bulk components of algae but percentages vary (5). As large percentage of growing tips of algae (7).
Lipase	Lipid (fat)	Appears to be found in most plants and animals (2) including algae (6) and bacteria (2). Small quantities in cell walls of algae (4). Forms 10% of body weight of mammals; reservoir of potential chemical energy (2, p. 476).

1. Kristensen 1972.
2. White, Handler and Smith 1968.
3. Meeuse 1962.
4. Kreger 1962.
5. Fowden 1962.
6. Benson and Shibuya 1962.
7. Huang and Giese 1958.

for it is improbable that lactose is a source of food for *Lingula*; Kristensen suggested that lactase in the systems of marine invertebrates may generally attack carbohydrates that have the same molecular linkage as lactose. I could find no information on inulase or its substrate. The indication of a weak laminaranase in the digestive diverticula of the articulate *Coptothyris* is interesting in view of the fact that laminaran is an important reserve in diatoms. However, this information on the strength of laminaranase (Sova *et al.* 1970) may be misleading; for although Sova *et al.* reported weak laminaranase activity in most invertebrates they studied, both Stone and Morton (1958) and Kristensen (1972) found the activities to be relatively strong in general. Methylcellulase (and undoubtedly methylchitinase) in invertebrates is poorly understood; although methylcellulose results only from the breakdown of cellulose, there is often no evidence of cellulase in invertebrate guts (see Barrington 1962; Kristensen 1972; Owen 1974); also there is usually no morphological evidence to indicate that invertebrate guts harbour large quantities of bacteria that are capable of hydrolysing cellulose (Kristensen 1972). There are many kinds of proteins and lipids in both plants and animals, and, as seen from Table 1, there is the possibility that brachiopods are only weakly able to assimilate some of these, and then only intracellularly. In considering these data on the distribution of proteases and lipases in *Lingula*, one should remember that concentration of extracellular enzymes may vary considerably with time in a single specimen if feeding processes are cyclic. One is also reminded of the negative results obtained in early attempts to determine extracellular proteases and lipases in the digestive tracts of bivalves (see Yonge 1923, 1926*a*); however, more recent techniques of enzyme determination, superior to those used by Yonge, should have been available both to Chuang, and to Kozlovskaya and Vaskovsky. The apparent lack of an extracellular lipase is supported by Chuang's (1959) observation that olive oil experimentally fed to *L. unguis* was digested only intracellularly. Perhaps brachiopods in general are unable, or only weakly able, to digest proteins and fats extracellularly; the information from Table 1, although scanty, suggests that possibility, for although tests on whole-animal tissues are probably inadequate for detecting weak enzymes, such tests should have indicated the presence of strong proteases in the articulate *Coptothyris*, if they had been present. Enzymes do occur in the intestinal epithelium of *L. unguis*, but these same enzymes are also found in other regions of the digestive tract, showing that matter that is digested in the intestine is also digested elsewhere. It is not known if enzymes in the intestine enable the inarticulates to digest a greater percentage of ingested material than the articulates, or if the articulates compensate for lack of intestinal digestion by relatively more complete digestion anteriorly.

The following general conclusions on brachiopod food can be drawn. In view of similar sizes of digestive cells, not only *L. unguis*, but brachiopods in general, probably cannot phagocytose particles more than about 2 μm across. Dissolved substances, colloidal material, and most bacteria are small enough to undergo intracellular digestion. It is known that dissolved material is used; and available enzyme information shows that dissolved carbohydrates can be absorbed through most of the gut epithelium. Indirect evidence from gut contents suggests that bacteria and/or colloids are also utilized. The apparent dominance of carbohydrases, both intracellular and extracellular, suggests that organic detritus may form a large percentage of the particulate material assimilated by brachiopods; organic detritus is high in carbohydrates and low in proteins and lipids (Agatova and Bogdanov 1972), while living material is high in proteins and low in carbohydrates and lipids (Parsons *et al.* 1961; Agatova and Bogdanov 1972); and the loosely compacted organic-mineral aggregates described by Rhoads (1973) and Johnson (1974) have been shown by Johnson (1974) to be largely carbohydrate. The frequent presence in invertebrate guts of methylchitinase in the absence of chitinase, and methylcellulase in the absence of cellulase, suggests that chitin and cellulose can be hydrolysed by bacteria in detritus; if so, methylchitinase in the absence of chitinase is another indication that organic detritus is a source of food for brachiopods. The strengths of extracellular amylase, and intracellular amylase, sucrase, and maltase indicate that algae form an important part of brachiopod food. The types of whole algae that can be digested must depend on structure and composition of their walls, on the presence of the necessary extracellular enzymes to break down these cell walls in the brachiopod gut, and on the rate of passage of the algae through the brachiopod gut. A weak laminaranase, if real, suggests that diatoms, often abundant in gut contents, are poorly utilized. Weak proteases, present only intracellularly, indicate that animal forms of life are not important foods for brachiopods and that proteins are probably obtained from other sources.

FOOD OF FOSSIL BRACHIOPODS

The trapping system of fossil brachiopods can be consistently interpreted to be functionally the same as in extant forms (Rudwick 1970, p. 145), and it is probable that the basic structure and functioning of the digestive system is essentially the same throughout the phylum. This degree of morphological uniformity is unlikely to be due to convergence, and is probably a reflection of common ancestry; in which case it can be inferred that the digestive system of brachiopods has remained essentially the same since the Lower Palaeozoic. All major categories of food of extant brachiopods (viz. dissolved substances, bacteria, colloids, organic detritus, and algae) were available throughout the Proterozoic. Thus it appears that the food of fossil brachiopods did not differ basically from that of Recent forms.

FUTURE WORK

Additional data on morphology, histology, physiology, and biochemistry would improve our knowledge of the food and feeding processes in brachiopods, in particular similarities and differences remain to be determined, especially between the inarticulates and articulates. Studies of water-flow around the filaments could determine the kinds of particles that are trapped under various conditions; investigations could ascertain the relative ease with which brachiopods hold motile and non-motile protistans. There is need for numerous studies of the alimentary tract, for example to determine the conditions under which ingested particles are released from the mucous cord for digestion, and faecal particles are rebound for expulsion; and to determine if feeding is cyclic (as it appears to be in filter-feeding bivalves) and whether the diverticular cells of brachiopods disintegrate periodically and shed their products into the stomach. The role played by phagocytes in digestion should also be examined. Further data on enzymes would be helpful in indicating what brachiopods can digest and where in their alimentary tracts different kinds of digestion occur: it would also be interesting to know where the extracellular enzymes are produced. More information on brachiopod food can be obtained from feeding experiments performed under controlled conditions. Further studies of uptake of dissolved material and transportation of nutrient products (McCammon and Reynolds 1972) are needed. To acquire direct evidence of what brachiopods are able to digest and the relative efficiencies of digestion of different substances, experiments could be performed similar to some of those of Ballantine and Morton (1956) on the bivalve *Lasaea rubra*. In these studies starved specimens should be fed different species of living micro-organisms, and the amount that is ingested then determined; at certain time intervals after feeding is started, contents from different parts of the gut and from faecal pellets should be examined to see how far digestion has proceeded in different areas. To determine if brachiopods consume bacteria that are on the surface of mud particles, experiments like Newell's (1965) are needed, where C/N ratios in bacteria-coated mud are determined before and after it passes through the gut. However, all these studies would only set constraints on the range of foods that can be utilized by brachiopods, but without such constraints we cannot judge from gut contents of recently collected animals, or from potential food in the environment, what brachiopods actually live on.

CONCLUSIONS

1. Methods of trapping food particles are nearly identical in all brachiopods.
2. Both inarticulates and articulates ingest and digest particulate material and expel particulate wastes.
3. Except in the expulsion of waste, nearly identical physiological processes appear to occur in the alimentary tracts of both kinds of brachiopods.
4. The articulate method of expelling waste through the mouth appears to have little disadvantage over the inarticulate method of expulsion through the anus.
5. The food of the two kinds of brachiopods is probably essentially the same.
6. Brachiopods are able to assimilate dissolved substances. Indirect evidence suggests that bacteria and colloids are also utilized; that organic detritus in general and some algae are important food sources; and that animal forms of life are not important foods for brachiopods.
7. There is no reason to suggest that the food of fossil brachiopods differed basically from that of extant forms.

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FLORA OF THE WEALDEN PLANT DEBRIS BEDS OF ENGLAND

by TIMOTHY C. B. OLDHAM

ABSTRACT. Descriptions are presented of forty-one cuticle species, all of probable gymnosperm origin, from the English Wealden. The distribution of these species and other plant remains within seventy-one plant debris beds from the Dorset, Isle of Wight, and Sussex Wealden is analysed. Significant groupings and associations, which to some extent reflect the differing ages of the material examined and perhaps also association in nature, are detailed together with stratigraphic conclusions. Palynological data from thirty of the samples show that miospore content is not directly related to the diversity and preservation state of the cuticle assemblage. The character of the plant debris beds suggests a probable origin in a delta top and/or shore-face and delta-front environment. The Wealden flora may be compared with certain aspects of the vegetation of southern Florida.

THE Wealden flora has previously been described by Seward (1894, 1895, 1913) and this work has been revised, in part, by Watson (1969) and Alvin (e.g. 1974 and earlier papers). The fossils described by Seward are of uncertain location but it appears that they were mostly collected from five beds within the Fairlight Clay formation that outcrops along the cliff section from Hastings to Pett Level in Sussex. The so-called Wealden flora is therefore little more than the megafossil remains found in the lowest formation of the outcrop as developed in Sussex. The other six more extensive formations that make up the Wealden deposits in the south-east of England and the entire successions developed in Dorset and the Isle of Wight are relatively undescribed botanically.

More extensive collection of megafossils over the wider area cannot remedy the situation as beds containing such remains are very few, as for example in the Fairlight Clay. Deposits producing identifiable miospores are not so restricted. Couper's (1958) paper on such fossils covers, if somewhat briefly, the entire Wealden groups, and Batten's (1973*a*, *b*, 1975) researches into palynological facies utilize material from much of the south-eastern succession. This work, while giving a general picture of the flora, is limited in its botanical application because of the difficulty in assigning dispersed miospores to megafossil genera.

There occur through the Wealden deposits plant beds that offer much of botanical interest although not usually containing any large plant remains. These beds have a high content of fragmented leaves and shoots, rarely greater than 10 mm in length. Such beds relate to those described as lignite beds by White (1921, 1928) and Arkell (1947) but this term does not apply to all the beds encountered as true lignite is sometimes rare or absent. The term 'plant debris bed' is considered to have a more useful application and is adopted in this paper.

The leaf and shoot fragments found within these beds are most satisfactorily prepared for examination by bulk maceration techniques. As a result of this it is the structure of the cuticle rather than gross morphological form that is apparent and the material is better regarded as dispersed plant cuticle than leaves and shoots as such.

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THE GEOLOGY

South-eastern England

The Wealden deposits may be divided into six or seven formations depending upon whether the Fairlight Clay and Ashdown Sand are treated as two formations or joined into one. Gallois (1965) follows the latter course but in this paper they will be treated as two formations following White (1928) as much attention is paid to the Hastings area where they are distinct.

The sediments of the Wealden group have been described by Allen (1959, 1967*a*, *b*), Taylor (1963), and White (1928).

The Wessex basin

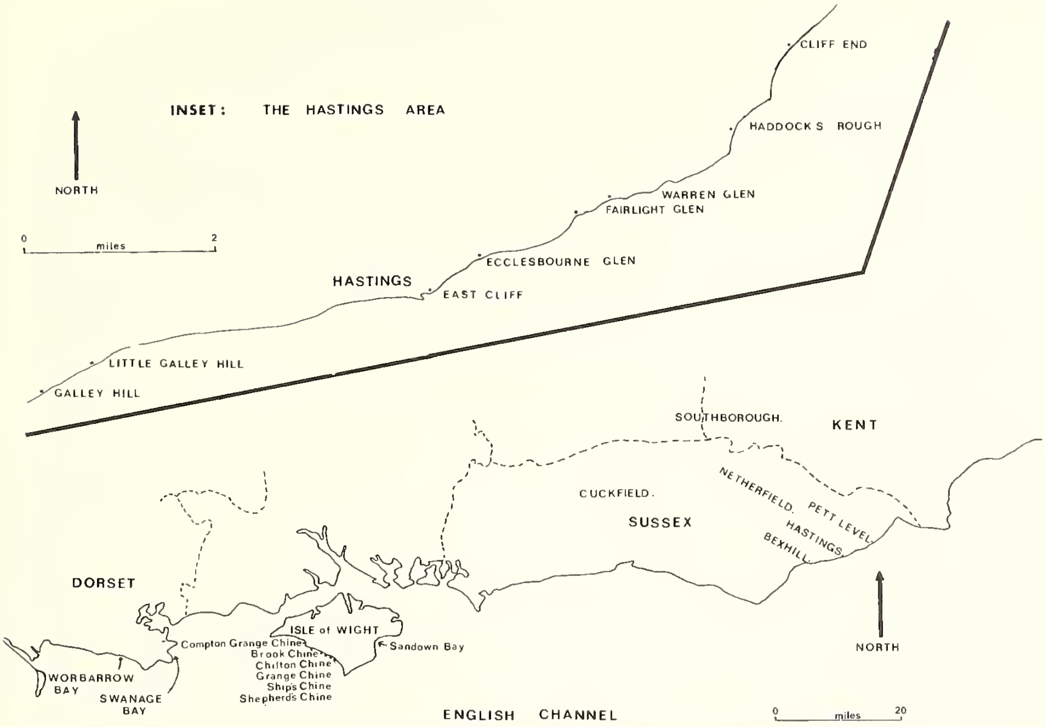
The two main areas of outcrop are in Dorset and the Isle of Wight. In both the sediments may be divided into two formations on lithological grounds; the Wealden Marls below and the Wealden Shales above. These sediments have received less attention than those of the south-eastern basin and the best descriptions remain those in the district memoirs of White (1921) and Arkell (1947).

In the Isle of Wight the beds outcrop in the south-western and south-eastern parts of the island where they are brought to the surface along the axes of two anticlinal folds. They occupy an area of less than 8 sq km and outcrop well only along the coast. They run for some 8 km between Compton Bay and Atherfield Point and for 1 km at Sandown Bay. Only the uppermost part of the Marls is exposed reaching a maximum development of 168 m (Arkell 1947). The Shales are better developed than in Dorset reaching a maximum of 60 m (Arkell 1947). The total thickness of Wealden sediment on the island, as revealed by the Arreton no. 1 Borehole, is 592 m (Falcon and Kent 1960).

The Marls consist of purple, red, green, and variegated clays with bands of sandstone. The absence of any band that can be traced over a considerable distance is particularly unfortunate as there are several faults that occur in the south-western section. Plant beds of the debris type are of regular occurrence especially on the south-western side of the island. Remains of vertebrates and molluscs occur. The Shales consist of stratified layers of dark clays with subordinate layers of clay-ironstone, sandstone, and shelly limestone. Plant remains, chiefly carbonized fragments of the fern *Weichselia reticulata*, occur rarely. Ostracods and molluscs dominate the fauna.

In Dorset the Wealden beds rest conformably upon the underlying Purbeckian strata. They exceed some 702 m thickness at Swanage but thin out westwards to 427 m at Worbarrow Bay and much less at Weymouth (Arkell 1947). Outcrops occur along the coast at Swanage Bay, Worbarrow Bay, Mupe Bay, Lulworth, and Durdle Door. The first two outcrops are the most useful as the sequence becomes increasingly confused westwards.

Lithologically and palaeontologically the Marls are similar to those of the Isle of Wight. Plant debris beds are slightly commoner but the fauna is less rich. As in the Isle of Wight there is rapid lateral variation of strata and correlation is difficult. Several bands of coarse quartz grit occur and according to Arkell (1947) one of these can be traced from Swanage to Durdle Door. The overlying Shales are poorly



TEXT-FIG. 1. Map of part of southern England showing the localities discussed in the text.

developed, being only 106 m thick at Swanage and absent at Worbarrow Bay. They resemble the Shales of the Isle of Wight but plant remains are rarer. Localities mentioned in the text are shown in text-fig. 1.

THE NATURE OF THE PLANT DEBRIS BEDS

Little has been written regarding the fragment composition of plant beds as opposed to their constituent floras, with the notable exception of coal strata. Harris (1953, 1963) refers to beds of dispersed plant fragments from the Jurassic of Yorkshire. He considers them to be mostly redeposited plant-bearing sediments of local origin, their constituent plants being of a rotted state prior to deposition and easily broken into small fragments as they were eroded out. His descriptions of the contents of these beds show them to be similar to those of the Wealden.

The distribution of the plant debris beds

They are best developed in the Fairlight Clay and Ashdown Sand formations of Sussex, especially along the cliff section from Hastings to Pett Level and at Galley Hill, Bexhill. They are, with the exception of beds of equisetalean remains, rare in the other formations of the Sussex Wealden. Some are found in the Tunbridge

Wells Sand but in the Wadhurst, Grinstead, and Weald Clay they appear to be absent. They are well distributed through the Wealden Marls of the Wessex basin but are not developed to any extent in the Wealden Shales.

Lithology

Beds containing small fragments of plant material can be found in most grades of sediment but where this is coarse the contained plant fragments are too poorly preserved to be of interest.

Medium to fine siltstones and claystones are the lithologies containing the better-preserved material. They are a medium to light-medium grey colour and often poorly consolidated. The best material comes from sediments soft enough to be cut with a knife.

Contents of the beds

Apart from the inorganic matrix, plant material is the sole component of the beds, animal remains not being found. The plant material consists of wood, both black and brown; cuticles of leaves, stems, and other plant organs; seeds; fruits; megaspores; miospores and charalean gyrogonites. The proportion of these varies from bed to bed. Miospores are usually the most important constituent in terms of number but rarely form much of the bulk of the bed. Wood also rarely forms the majority of the bulk and when it does plant cuticle material is scarce and the deposits are better termed lignite beds. Seeds and fruits are of little importance as are gyrogonites. Megaspores bear an inverse relationship to the richness of the cuticle remains but are normally present if only in small numbers.

It is the presence of large amounts of cuticular material that characterizes these beds and sets them apart from the lignite beds on the one hand and the megafossil beds on the other. This distinction is not absolute and a continuum of variation can be found. The cuticular material varies in size both within and between beds but is generally between 2 and 5 mm and rarely exceeds 10 mm. The material consists chiefly of leaves and pinnae but material relating to stems and reproductive structures also occurs. The leaf remains are usually fragmentary but occasionally complete leaves and sometimes branches can be seen.

Structure of the debris beds

Most of the beds comprise a complex of numerous individual beds, the whole structure ranging from a few centimetres to several metres in thickness. Isolated individual beds are rare. These complexes are separated by tens or even hundreds of metres of barren sediment.

The distinction of different sorts of debris beds

It was not considered wise to divide the beds up into different sorts as they varied along several independent parameters. These include the development of laminae, the proportion of plant material to inorganic matrix, the degree of cohesion of the matrix, the state of preservation of the contained plant material, the diversity of the contained plant matter, the amount of wood present, and the size of the cuticle fragments.

MATERIALS AND METHODS

Seventy-one samples from the plant debris beds of the Wealden group were examined in detail. These were collected from outcrops except for six samples from the Cuckfield no. 1 Borehole. Full details of the lithology and location of each of the samples is supplied in the appendix.

The methods employed in preparing the samples for examination were simple and gentle as much of the material was fragile. The samples were placed in 10 vol. hydrogen peroxide for an hour and the resulting slurry was sieved (250 μm sieve) and washed. The material remaining was placed in cold 60% hydrofluoric acid for three days and then sieved and washed as before. The mineral-free plant material that remained was cleaned by oxidation; 50 ml of concentrated nitric acid was added to 25 g of plant material. The length of time the material was left in the acid varied from sample to sample but twenty-four hours was usually the optimum time. The plant material was then again washed and placed in 5% ammonium hydroxide for ten minutes. After a final wash it was suitable for microscopic examination.

Individual specimens were mounted in 'Clearcol' and 'DePeX'. For examination under the scanning electron microscope specimens were mounted on 12 mm diameter aluminium stubs using 'Durofix' as the adhesive and 40% gold/palladium as the coating medium. Samples used for recording the miospore content were prepared following the methods of Dettmann (1963, p. 11).

SYSTEMATIC TREATMENT OF THE DISPERSED CUTICLES

The nature of the taxa

The taxa described are based upon the structure of the cuticle of plant organs; the cuticle being taken as the cutinized part of the epidermis and hypodermis. With much of the material gross morphological features could not be determined and what little information was available has been treated separately from the main diagnoses.

Each taxon is based upon ten, or in thirteen cases, five specimens, all from the same sample. Similar specimens from other samples are treated separately under comparison records, and so the taxa could be regarded as biorecords and not species in the usually accepted sense. The taxa are characterized by a serial number which would be prefaced by an author identifier outside this paper, an informal classificatory guide and the author's informal working reference (Hughes and Moody-Stuart 1967*b*, 1969).

Systematic position of the taxa

Three factors contrive to make it difficult to place every taxon within the existing hierarchical framework. First, few megafossil leaf taxa are based on cuticle characters alone, and many species have been described without reference to the cuticle at all. Second, a combination of cuticle features does not necessarily characterize a particular family or order. It is not therefore possible to place every taxon within even a major group. Third, the cuticle that can be prepared from the plant debris beds is often of considerably superior preservation and of a larger size than that which can be prepared from the megafossil leaves that form the basis of Seward's work. The diagnosis of a cuticle taxon will therefore differ somewhat from that of the cuticle prepared from a megafossil leaf even if they are of the same species.

Unsatisfactory though this may be, in practice most of the cuticle species can be referred to an order and often a leaf genus, but the slightly unusual taxonomic approach has been used for the reasons explained above.

The choice of cuticle characters

Thomas (1930), Florin (1931, 1958), and Harris (1932) have all considered the problem of the constancy of cuticle characters amongst the gymnosperms. They conclude that the cuticle is well suited to delimiting species and often genera and more rarely the larger taxonomic groupings. Meyen (1965) lists fifteen taxonomically important features of the cuticle, laying stress on those associated with the stomata.

All available features of the cuticle have been used in the diagnoses of the cuticle taxa presented here but the following requirements have been found necessary in order that the diagnosis can be considered reliable:

1. Preservation of the specimens must be sufficiently good to allow all structures to be clearly seen.
2. Stomata must be present.
3. A sufficiently large piece of cuticle must be available so that such features as stomatal arrangement can be determined.
4. Ten, or at the very least, five, specimens should be used for each diagnosis.
5. Preferably both surfaces of the leaf should be available for study.

SYSTEMATIC SECTION

Forty-one cuticle species are described, one from the Purbeck beds of Netherfield, twenty-five from the Fairlight Clay of the Hastings area, one from the Ashdown Sands of the Hastings area, twelve from the Wealden Marls of Dorset, and two from the Wealden Marls of the Isle of Wight. Only an outline is presented; full details of the diagnoses are deposited with the British Library, together with an explanation of the terms and abbreviations used (NLL SUP 14006).

The order and circumscription of the taxa is that adopted by Engler (1954). Sample details are given in the appendix (pp. 500–502).

GYMNOSPERMAE
Class CYCADOPSIDA
Order CAYTONIALES

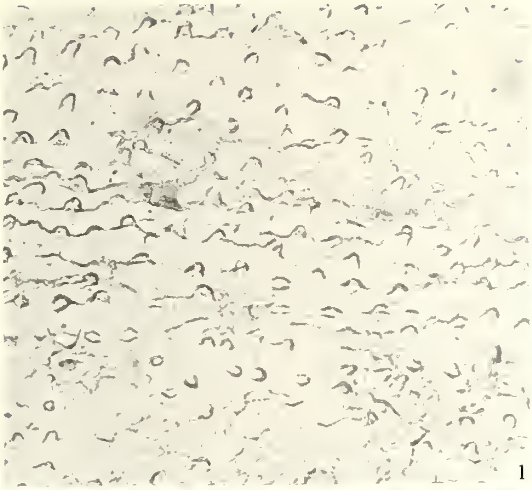
This is an isolated order with a single leaf genus, *Sagenopteris* Presl in Sternberg 1838. Two species have been described from the English Wealden, *S. mantelli* (Dunker) Schenk and *S. acutifolia* Seward.

EXPLANATION OF PLATE 55

Figs. 1–4. 1 CAYT SaA. 1, ×500, LM., surface 2, stomata and papillae; P25: 5/2.2. 2, ×1000, SEM., surface 2, inside, stoma; B58. 3, ×500, SEM., surface 2, outside, papillae; B58. 4, ×500, SEM., surface 2, inside, epidermal cells, hypodermis; B58.

Figs. 5–8. 2 CYCAD PsA. 5, ×150, LM., surface 2, stomata; P49: 24/2. 6, ×500, LM., surface 2, stoma; P49: 24/2. 7, ×1000, SEM., surface 2, outside, stomatal apertures; B38. 8, ×1000, SEM., surface 2, inside, stoma; B38.

PLATE 55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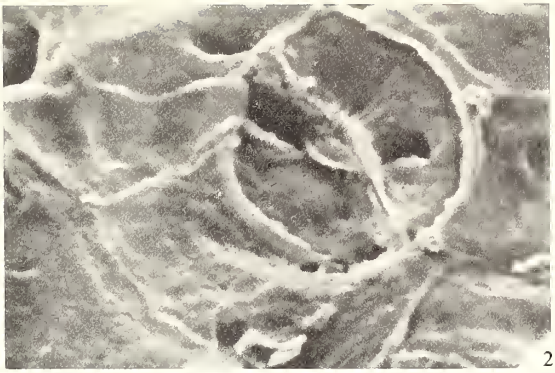
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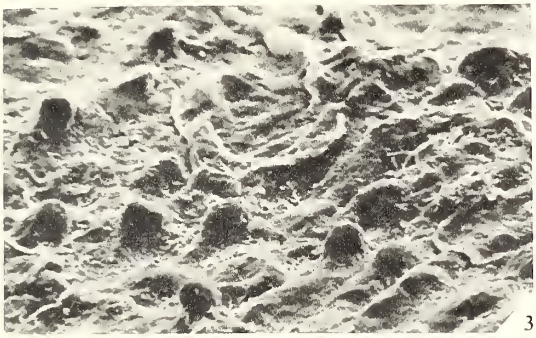
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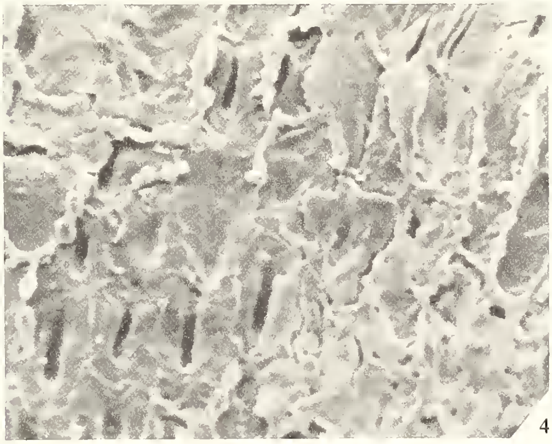
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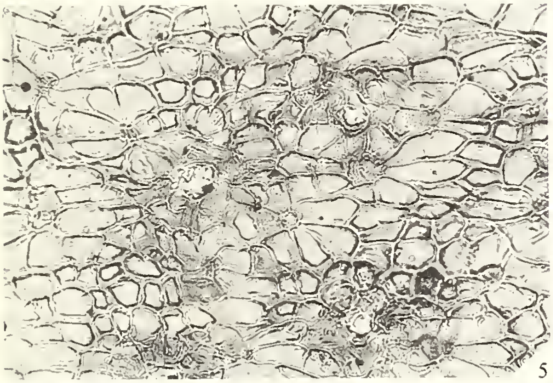
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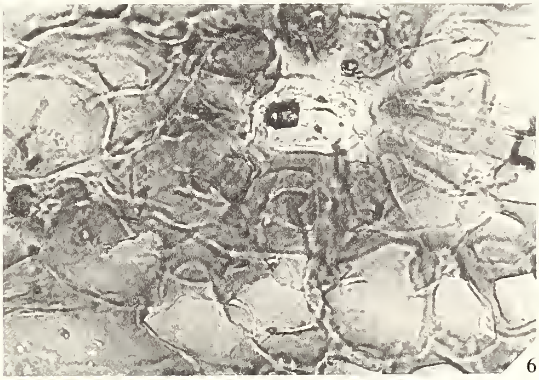
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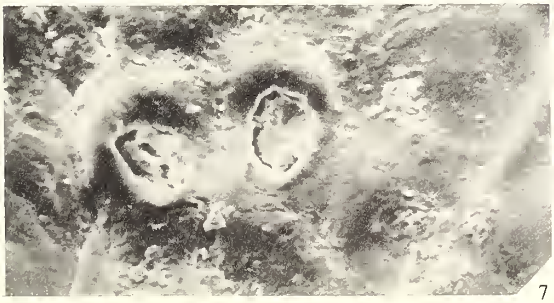
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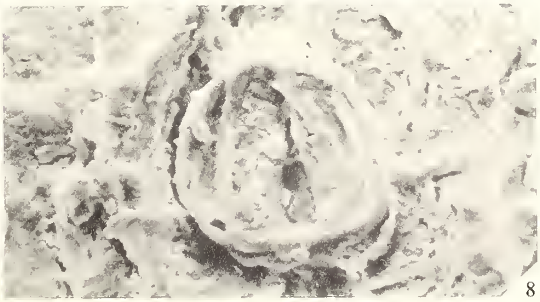
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OLDHAM, 1 CAYT SaA and 2 CYCAD PsA

Cf. Genus SAGENOPTERIS Presl
1 CAYT SaA

Plate 55, figs. 1–4

Record sample. Ashdown Sand, Sample no. 7AH. From 300-mm plant debris bed complex, medium grey, fine siltstone, plant material in fine laminae. Ten specimens, P25: 5/2.1, 3.1, 4.1, 2.2, 4.2; 7/1.2; 17/2.1, 4.1, 1.2, 2.2.

Systematic position. The characters of the cuticle, especially the stomata, closely resemble those of the genus *Sagenopteris*. Jongmans and Dijkstra (1964) list over sixty species belonging to the genus. Of these cuticle is only known for six species and only one of these, *S. mantelli*, occurs in rocks of a relevant age. Carpentier (1939) describes the cuticle of this species and it differs from 1 CAYT in having no papillae and distinct subsidiary cells. *S. hallei* Harris is the only species with papillae in large numbers but it is a Liassic species and differs in several respects from 1 CAYT. *S. acutifolia*, the only other species recorded from the English Wealden, has not yielded any cuticle.

Order CYCADALES–NILSSONIALES

These two orders are not clear cut in terms of cuticle characters and so will be considered together. There are a considerable number of Mesozoic leaf genera belonging to this group and five of these have been recorded from the English Wealden. It is possible that some of the taxa described under this heading relate to the pteridosperms rather than the cycads but the two groups cannot be differentiated on cuticle characters alone.

Cf. Genus PSEUDOCTENIS Seward
2 CYCAD PsA

Plate 55, figs. 5–8

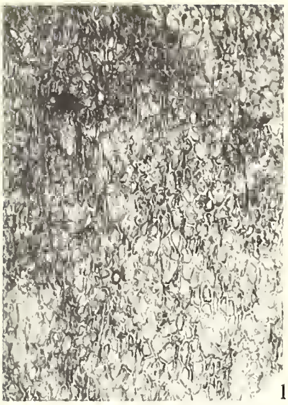
Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 20/1; 24/1, 2, 3; 25/1, 2, 3; 26/1, 2, 3.

Systematic position. It relates to the cuticle of *Pachypteris* Brongniart to some extent but does not agree with *P. lanceolata* Brongniart, the single English Wealden species of this genus, nor does it agree in all respects with any member of that genus that has been described with reference to cuticle characters. Its resemblance to *Pseudoctenis* is also close, although this genus is hypostomatic as defined by Harris. Seward (1913) lists one specimen of *P. earthiensis* (Richard) Seward from Ecclesbourne Glen but it has not yielded cuticles. Carpentier (1939) describes a species of *Pseudoctenis*

EXPLANATION OF PLATE 56

Figs. 1–4. 3 CYCAD PsB. 1, ×50, LM., general view; P127: 7/1. 2, ×2000, SEM., surface 2, inside, stoma; B28. 3, ×1000, SEM., surface 2, outside, stomatal aperture; B28. 4, ×1000, SEM., surface 2, inside, epidermal cells and hypodermis; B28.

Figs. 5–8. 4 CYCAD CtA. 5, ×50, LM., both surfaces, general view; P59: 20/1.1. 6, ×150, LM., surface 2, stomata; P59: 20/1.1. 7, ×500, LM., surface 2, stomata; P59: 20/1.1. 8, ×150, LM., surface 1, epidermal cells and thickened cells; P59: 20/1.1.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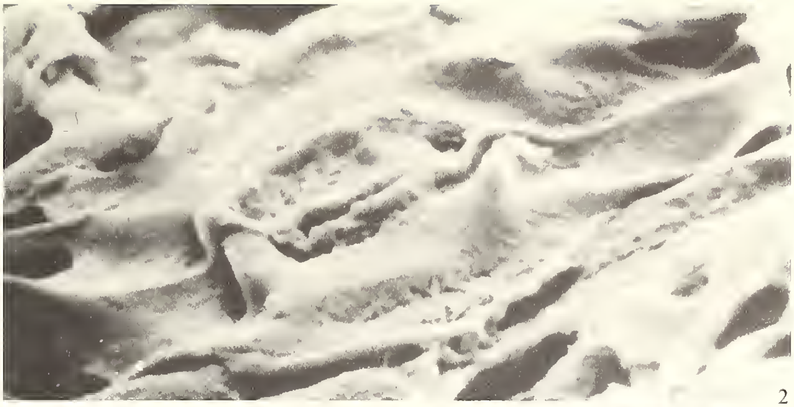
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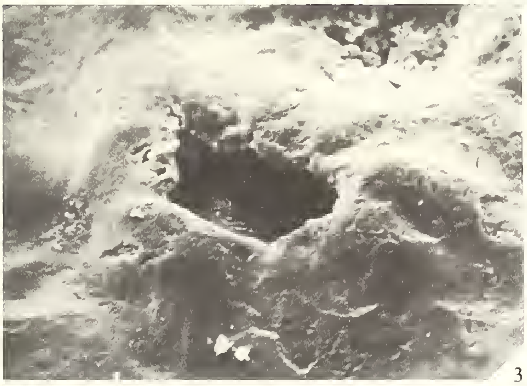
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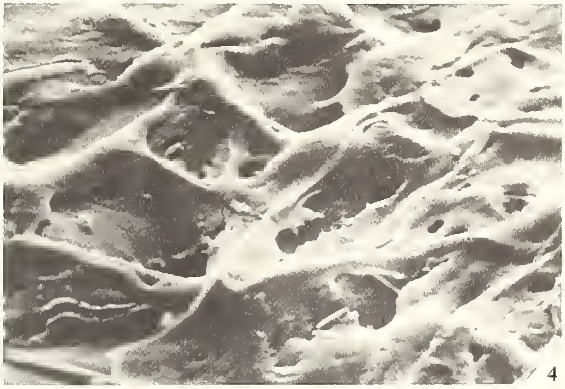
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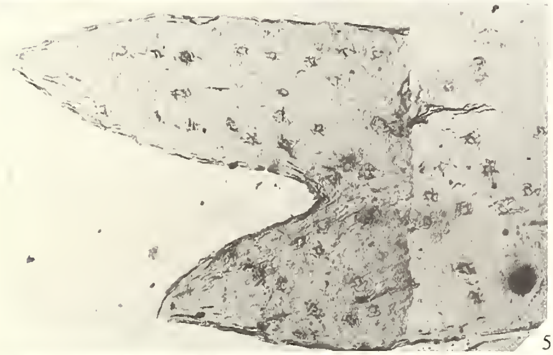
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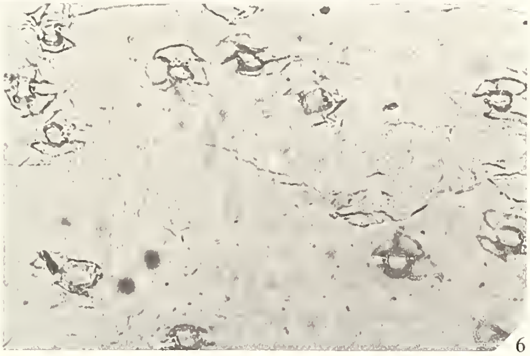
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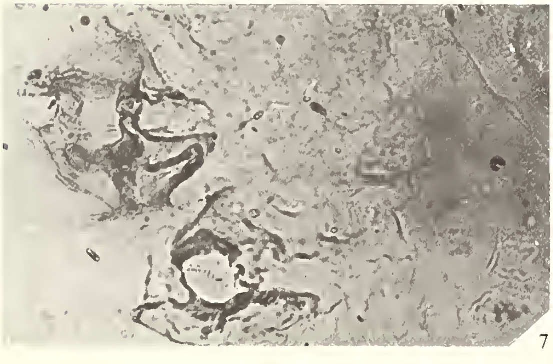
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8

OLDHAM, 3 CYCAD PsB and 4 CYCAD CtA

giving full details of the cuticle structure from the French Wealden; this is similar to, but not the same as, 2 CYCAD. The same can be said of the *Pseudoctenis* species described by Benda (1961) from the German Wealden. The lack of evidence concerning the gross morphology of 2 CYCAD would make the placing of it in the genus *Pseudoctenis* premature.

3 CYCAD PsB

Plate 56, figs. 1–4

Record sample. Wealden Marls, Sample no. 27BD. From 100-mm band in 1-m plant debris bed complex, light grey, fine siltstone, plant material in irregular laminae. Ten specimens, P127: 5; 6; 7; 8; 9; 11; 12; 13; 14; 15.

Systematic position. This taxon is close to 2 CYCAD and remarks made with regard to its systematic position apply here.

Cf. Genus CTENIS Lindley and Hutton

4 CYCAD CtA

Plate 56, figs. 5–8; Plate 57, figs. 1, 2

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Ten specimens, P59: 16/3.2, 4.1; 20/1.1, 2.1, 2.3, 3.1; 23/2.3; 25/2.1, 2.2; 27/1.1.

Systematic position. This taxon is close to the genus *Ctenis*, important points of similarity being the structure and thickening of the guard cells and subsidiary cells. The major point of disagreement is the large number of stomata on both surfaces of 4 CYCAD and their virtual restriction to the lower surface in *Ctenis*. In its stomatal distribution 4 CYCAD bears some resemblance to *Stenopteris* Saporta but it differs in stomatal structure.

5 CYCAD CtB

Plate 57, figs. 3–6

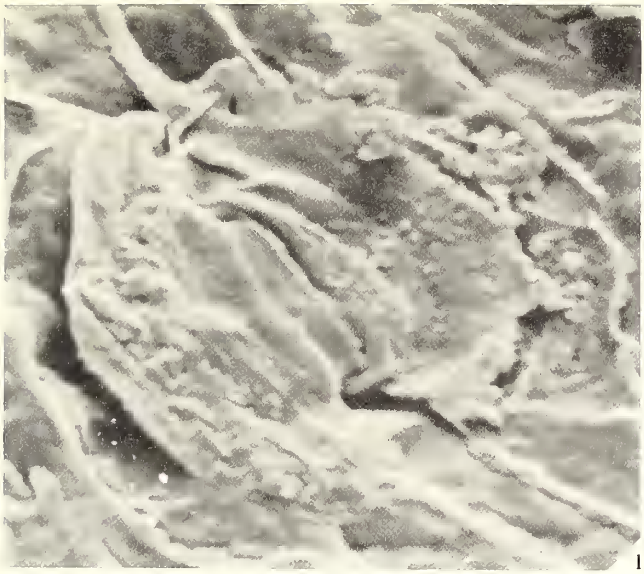
Record sample. Wealden Marls, Sample no. 18DD. From a 75-mm band in plant debris bed complex, light medium-grey claystone, plant material irregularly dispersed through the matrix. Ten specimens, P118: 1/4.2; 3/2.1; 5/4.1; 6/1.1, 4.1; 7/3.2; 11/4.1; 12/2.1, 2.2.

Systematic position. This taxon is close to 4 CYCAD and remarks made concerning the affinity of that taxon apply here. In its lack of stomata on one surface it is, however, even closer to the genus *Ctenis*.

EXPLANATION OF PLATE 57

Figs. 1–2. 4 CYCAD CtA. 1, × 1000, SEM., surface 2, inside, stoma; B42. 2, × 1000, SEM., surface 1, inside, thickened cells; B42.

Figs. 3–6. 5 CYCAD CtB. 3, × 1000, SEM., surface 2, inside, stoma; B56. 4, × 150, LM., surface 1, epidermal cells; P118: 6/4.1. 5, × 500, LM., surface 2, stoma; P118: 6/4.1. 6, × 500, SEM., surface 1, inside, epidermal cells; B56.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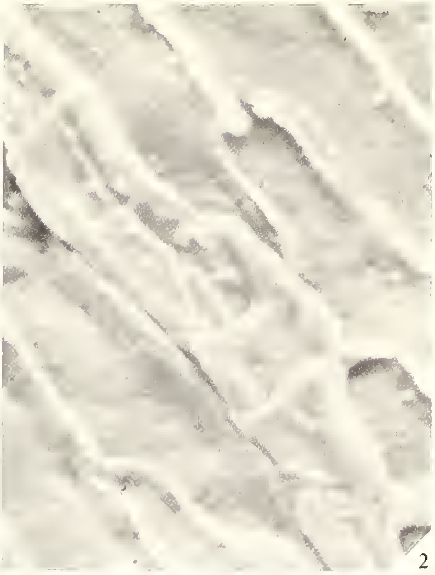
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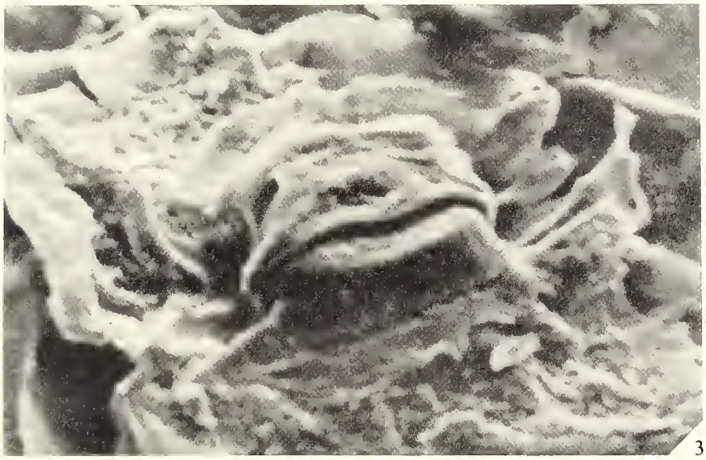
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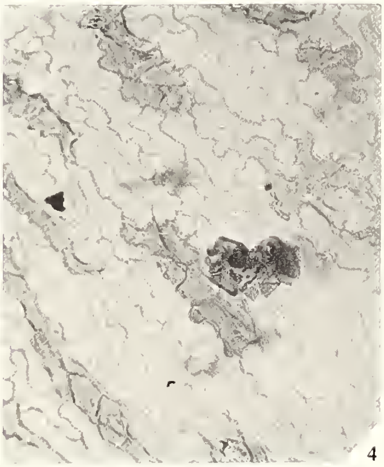
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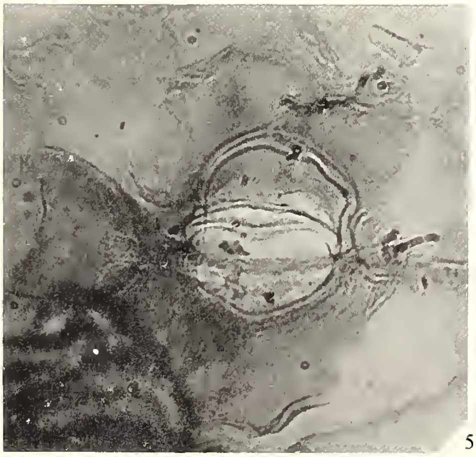
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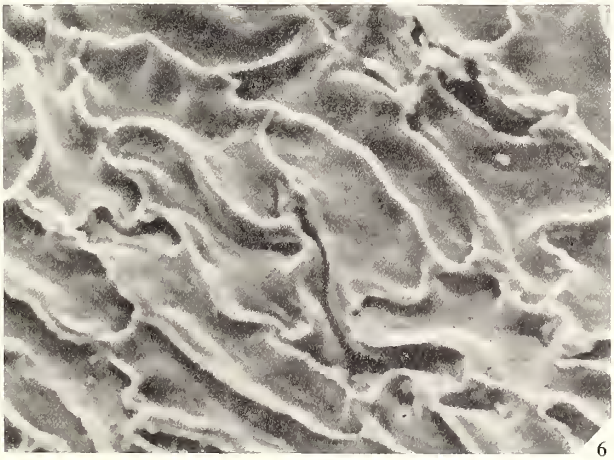
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OLDHAM, 4 CYCAD CtA and 5 CYCAD CtB

Cf. Genus ALMARGEMIA Florin
6 CYCAD AlA

Plate 58, figs. 1–3

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 11/3.1; 20/3.2; 38/1.1, 1.3, 4.1.

Systematic position. This taxon agrees well with the diagnosis of the genus *Almargemia* Florin. The two species in the genus are *A. dentata* Florin from the Aptian of Portugal and *A. incrassata* Archangelsky from the Tico flora. 6 CYCAD has the characteristic rows of thickened cells of *A. incrassata* and has similar thickenings on the guard cells. The main point of divergence is the size of the subsidiary cells which are considerably smaller in 6 CYCAD. The genus *Stenopteris* is also similar but none of the published species agree with 6 CYCAD.

7 CYCAD AlB

Plate 58, figs. 4–8

Record sample. Fairlight Clay, Sample no. 18AH. From a 74-mm band in plant debrid bed complex, medium dark-grey siltstone plant material in laminae. Ten specimens, P81: 11/1.1, 2.1; 23/3.1; 25/1.2; 27/2.2; 28/1.2; 30/2.2, 3.2; 32/2.1; 34/4.1.

Systematic position. This taxon is close to 6 CYCAD in its stomatal structure and is likely to be of cycadalean affinity. It is not as close to *Almargemia* as 6 CYCAD.

8 CYCAD CeA

Plate 59, figs. 1–4

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 35/1.1, 2.1, 2.2; 59/1.1, 1.2, 1.3, 2.1, 2.2, 2.3.

Systematic position. This taxon is close to 9 CYCAD. The characteristic ring around the stomatal aperture is reminiscent of *Ctenozamites* and it agrees well with the diagnosis of that genus except in the factor of the stomata on both surfaces. A thickened ring is also characteristic of the genus *Mesosingeria* Archangelsky from the Tico flora, but it differs in other respects.

9 CYCAD CeB

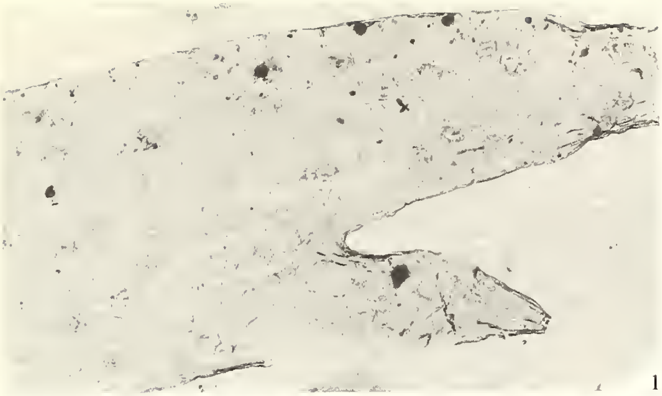
Plate 59, figs. 5–8

Record sample. Wealden Marls, Sample no. 7DD. From 75-mm band in plant debris bed complex, plant material irregularly dispersed through the matrix. Ten specimens, P100: 1/1.2; 2/3.1, 4.2; 4/3.2; 7/2.1; 8/1.1, 1.2; 10/1.1, 1.2; 11/3.1.

EXPLANATION OF PLATE 58

Figs. 1–3. 6 CYCAD AlA. 1, ×50, LM., both surfaces, general view; P59: 41/1.1. 2, ×150, LM., surface 2, stomata; P59: 41/1.1. 3, ×500, LM., surface 2, stoma; P59: 41/1.1.

Figs. 4–8. 7 CYCAD AlB. 4, ×500, SEM., surface 2, outside, papillae; B55. 5, ×150, LM., surface 2, stomata and papillae; P81: 11/2.1. 6, ×2000, SEM., surface 2, inside, stoma; B55. 7, ×150, LM., surface 1, epidermal cells; P81: 11/2.1. 8, ×1000, SEM., surface 1, inside, epidermal cells; B55.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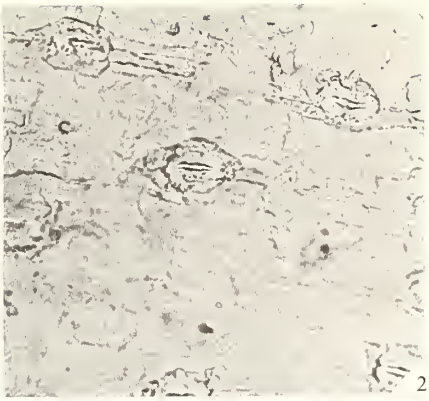
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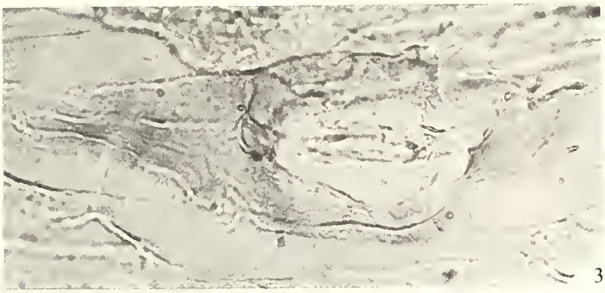
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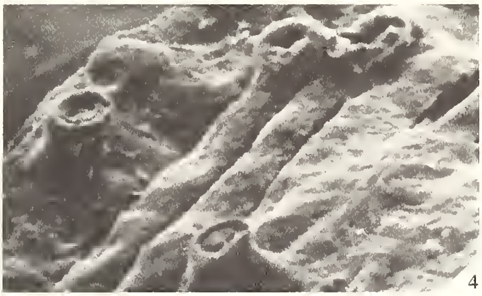
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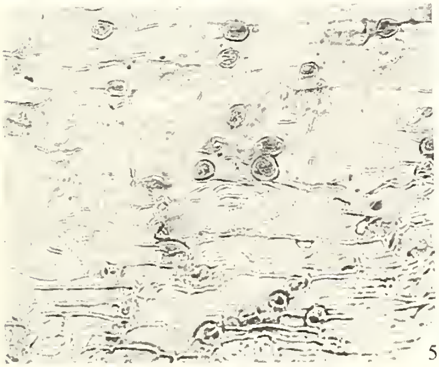
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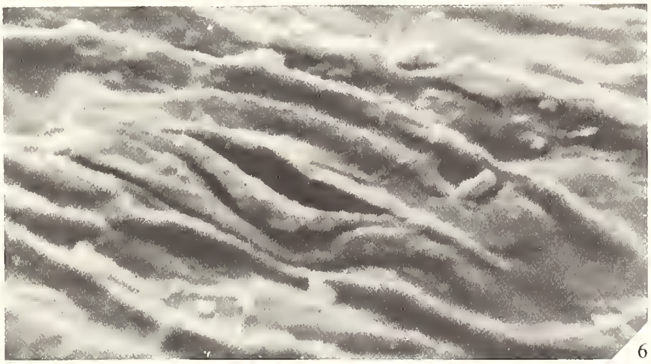
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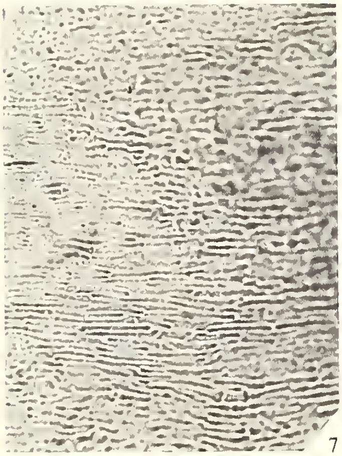
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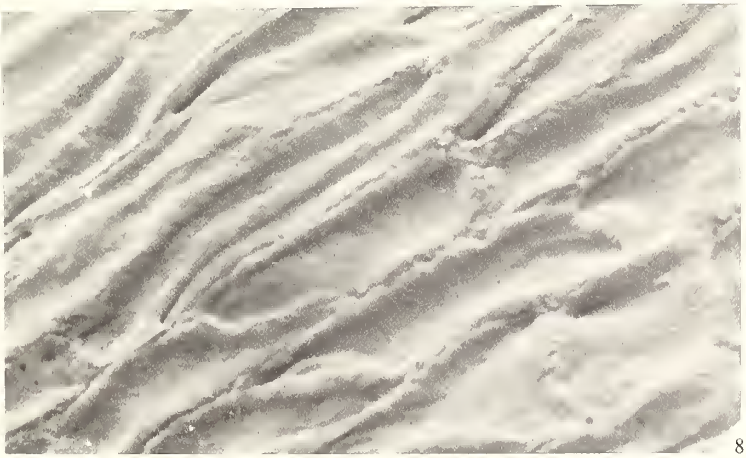
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OLDHAM, 6 CYCAD AlA and 7 CYCAD AlB

Systematic position. It is close to 8 CYCAD and remarks made concerning the affinity of that taxon apply here. Benda (1961) describes a cuticle which he does not place in any genus but refers to as Cycadee Form L; this appears very similar to 9 CYCAD.

Cf. Genus BECKLESIA Seward
10 CYCAD BeA

Plate 60, figs. 1–6

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 30/1.3; 31/1.1, 2.1, 2.2; 32/1, 2, 4; 48/2.1; 49/2.1.

Systematic position. Seward erected the genus *Becklesia* in 1895 and placed it in Gymnospermae incertae sedis. He described one species from the English Wealden, *B. anomola.* This species has been revised by Watson (1969) and in the same work she defines a new species from leaf fragments, *B. sulcata.* This is undoubtedly the same as 10 CYCAD.

11 CYCAD BeB

Plate 61, figs. 1–4

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Nine specimens, P49: 30/2; 32/3; 49/2.2; 51/1.2; 56/2.1, 2.2; 57/2.1; 58/2.

Systematic position. This is close to 10 CYCAD but does not agree completely with any of the published species of the genus *Becklesia.*

12 CYCAD BeC

Plate 61, figs. 5–9

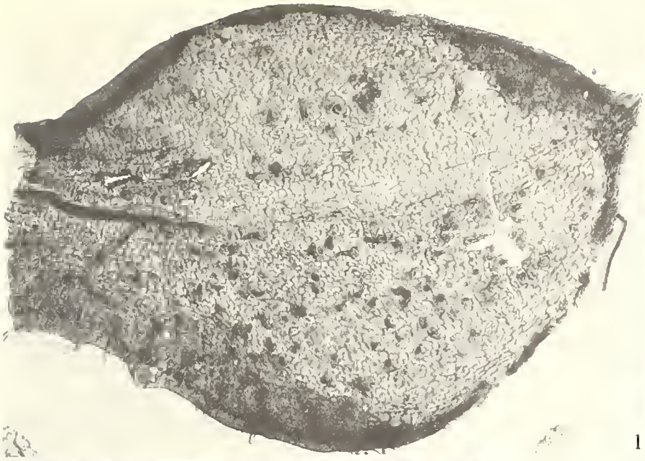
Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material concentrated in laminae. Ten specimens, P98: 2/4.1; 6/1.1, 1.2; 14/1.2, 2.2, 2.1; 15/1.1; 19/1.1, 3.2; 23/3.2.

Systematic position. This is close to 10 CYCAD and 11 CYCAD and remarks made concerning the affinity of those taxa to the genus *Becklesia* apply here. Like 11 CYCAD it does not agree completely with any of the published species of the genus.

EXPLANATION OF PLATE 59

Figs. 1–4. 8 CYCAD CeA. 1, ×50, LM., surface 2, general view; P49: 59/2.1. 2, ×150, LM., surface 2, hairs, papillae, and stomata; P49: 59/2.1. 3, ×2000, SEM., surface 2, outside, stomatal aperture; B41. 4, ×500, LM., surface 2, stoma; P49: 35/2.1.

Figs. 5–8. 9 CYCAD CeB. 5, ×150, LM., surface 2, stomata; P100: 2/3.1. 6, ×1000, SEM., surface 1, inside, epidermal cells; B48. 7, ×1000, SEM., surface 2, inside, stoma; B48. 8, ×1000, SEM., surface 2, outside, stomatal aperture; B48.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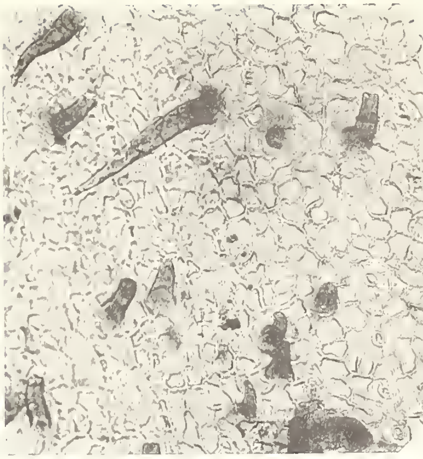
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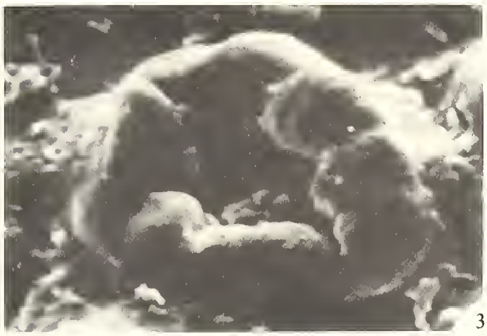
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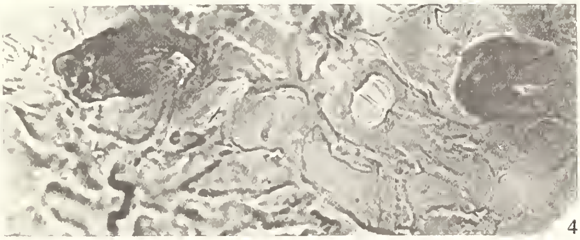
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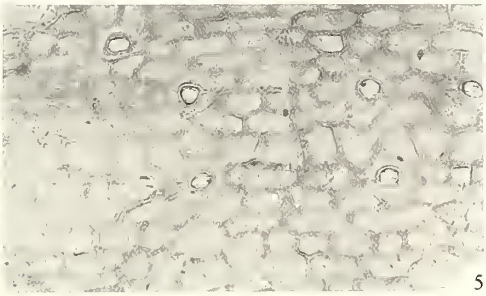
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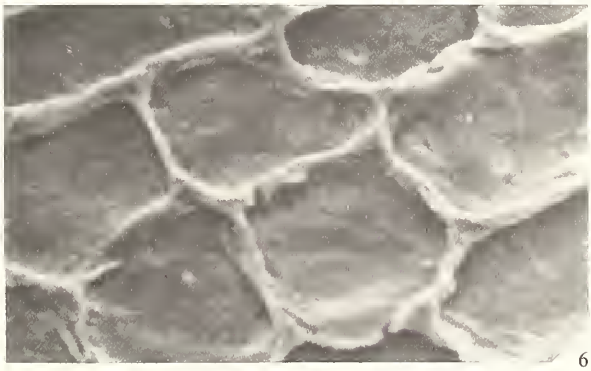
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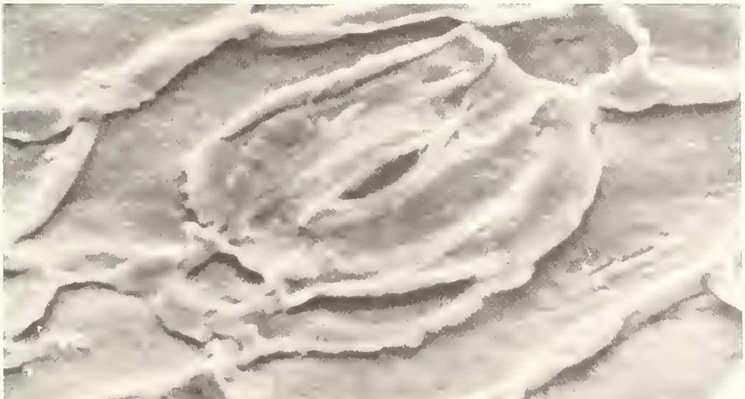
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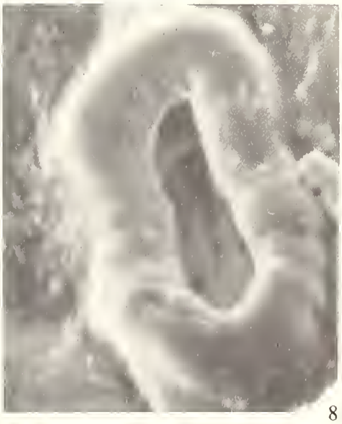
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OLDHAM, 8 CYCAD CeA and 9 CYCAD CeB

Order BENNETTITALES

This group is well defined as a whole on cuticle characters but as Harris (1969) states there are no styles of cuticle-characterizing genera. The division into genera is on gross morphology although a few genera such as *Pseudocycas* and *Pterophyllum* can be identified without recourse to such information. The lack of information regarding the cuticle of the bennettitalean species described by Seward from the Wealden makes the task of placing isolated cuticles in their correct leaf genera more difficult.

Cf. Genus PSEUDOCYCAS Nathorst

13 BENN PeA

Plate 62, figs. 1–3

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 40/1.2, 2.1, 2.2; 55/2.1, 3.1.

Systematic position. The presence of a stomatal groove places it within the genus *Pseudocycas*. It agrees well with *P. saportae* (Seward) Holden from Ecclesbourne and Hastings and an examination of the type material confirms this agreement.

14 BENN PeB

Plate 62, figs. 4–7

Record sample. Fairlight Clay, Sample no. 34AH. From 150-mm plant debris bed complex, medium light-grey siltstone, plant material in laminae. Ten specimens, P64: 4/1.1, 2.1, 1.2; 7/1.1, 2.1, 1.2, 2.2; 8/2.1; 9/2.2; 10/2.1.

Systematic position. Its cuticle characters and the possession of a stomatal groove places it in the genus *Pseudocycas*. It does not agree with any of the published species of this genus.

Cf. Genus ZAMITES Brongniart

15 BENN ZaA

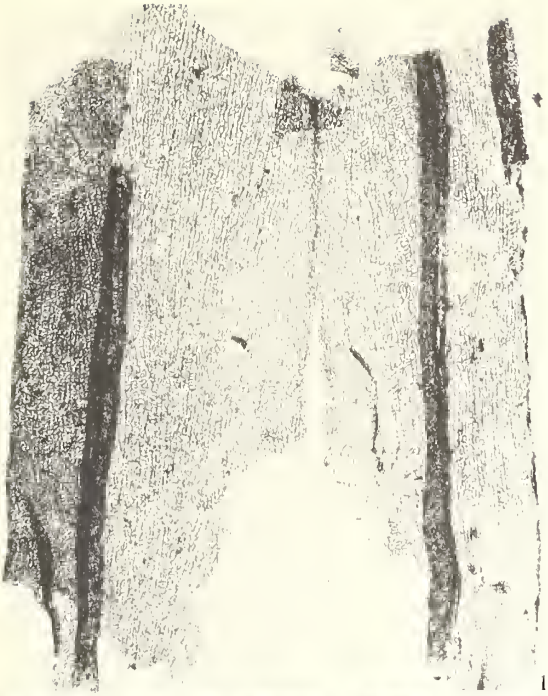
Plate 63, figs. 1–3

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 14/1.1; 34/1.2, 2.1; 36/2.2, 4.2; 37/2.2; 55/1.3; 60/1.1; 62/3.2; 63/3.2.

Systematic position. This taxon is close to the cuticles of specimens BMNH V2363, BMNH V2262, and BMNH V2698 which Seward included in *Zamites buchianus*. Some other specimens placed by Seward in the same species have totally different cuticles.

EXPLANATION OF PLATE 60

Figs. 1–6. 10 CYCAD BeA. 1, ×20, LM., both surfaces, general view; P49: 32/4. 2, ×100, SEM., surface 2, outside, groove; B50. 3, ×1000, SEM., surface 2, inside, stoma; B22. 4, ×500, LM., surface 2, stomata; P49: 32/1. 5, ×500, SEM., surface 2, inside, epidermal cells; B22. 6, ×500, SEM., surface 1, inside, epidermal cells; B22.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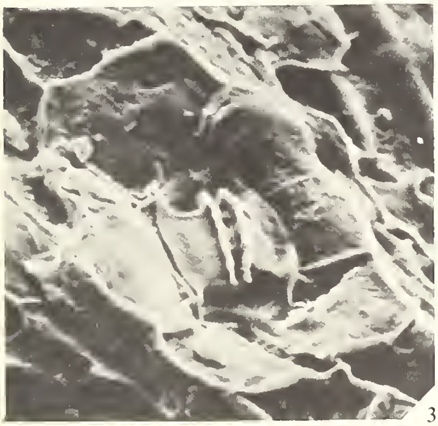
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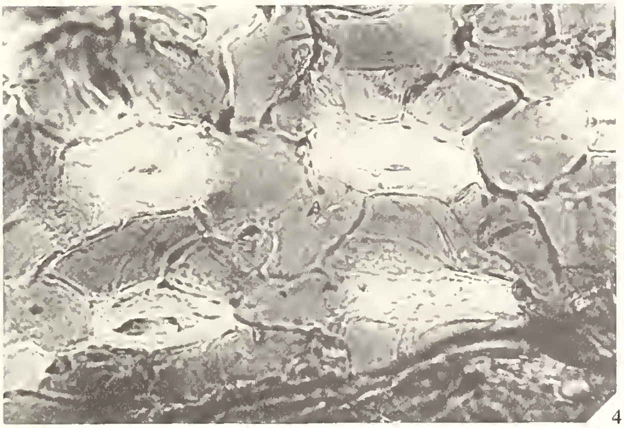
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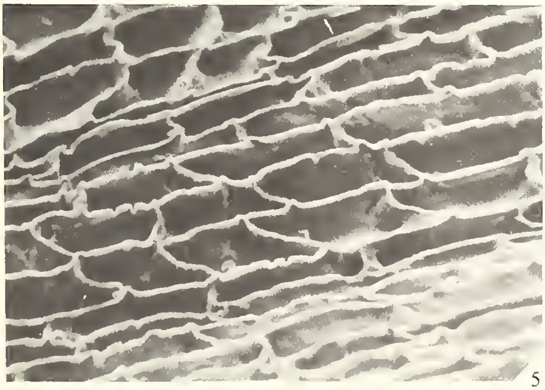
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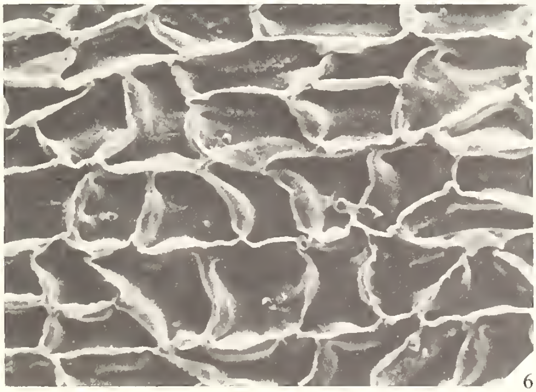
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OLDHAM, 10 CYCAD BeA

16 BENN ZaB

Plate 63, figs. 4–7

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 36/3.2; 37/2.1; 61/3.3; 63/1.3, 3.1.

Systematic position. This relates well to the cuticle of specimens BMNH V2741 and BMNH V2360 which Seward placed in the species *Otozamites goppertianus.* It also resembles Daber's (1960) Blattfragment G which he does not place in any genus.

17 BENN ZaC

Plate 64, figs. 1–5

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 34/3.1; 36/2.1, 4.2; 37/3.1; 63/2.1.

Systematic position. This taxon does not resemble the cuticles of any Wealden bennettitalean leaves examined. Its closeness to 15 BENN and 16 BENN, however, suggests an affinity with *Zamites.*

Cf. Genus OTOZAMITES Braun
18 BENN OtA

Plate 64, figs. 6–8

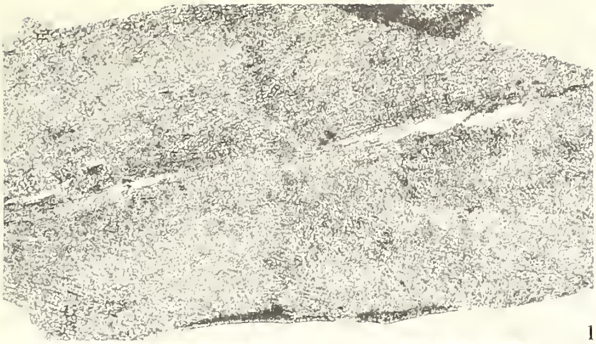
Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band plant in debris bed complex, light-grey siltstone, plant material in irregular laminae. Ten specimens, P59: 15/2.2; 16/4.2; 17/1.1, 1.3; 22/1.2; 35/1.3; 36/3.1; 37/1.2, 3.1, 4.2.

Systematic position. This taxon agrees well with the cuticle of specimen BMNH V21222 which Seward places in *O. klipsteinii* var. *longifolia.* It also agrees with specimen BMNH V21222a which Seward places in *O. klipsteinii* var. *superba.* Unfortunately it also agrees with the cuticle of specimens BMNH 2123c and BMNH V2123d which Seward places in *Z. carruthersi* and with specimen BMNH V2120 which he places in *Z. buchianus.* This underlines the need for a thorough revision of Wealden bennettitalean leaves.

EXPLANATION OF PLATE 61

Figs. 1–4. 11 CYCAD BeB. 1, ×20, LM., surface 1, general view; P49: 53/1.1. 2, ×500, SEM., surface 1, inside, epidermal cells; B64. 3, ×150, LM., surface 2, groove; P49: 32/3. 4, ×500, LM., surface 2, stoma; P49: 32/2.

Figs. 5–9. 12 CYCAD BeC. 5, ×1000, SEM., surface 2, inside, stoma; B53. 6, ×150, LM., surface 2, groove; P98: 19/3.2. 7, ×50, LM., surface 1, epidermal cells; P98: 19/3.2. 8, ×500, SEM., surface 2, inside, epidermal cells and stomatal groove; B53. 9, ×500, SEM., surface 2, outside, groove; B53.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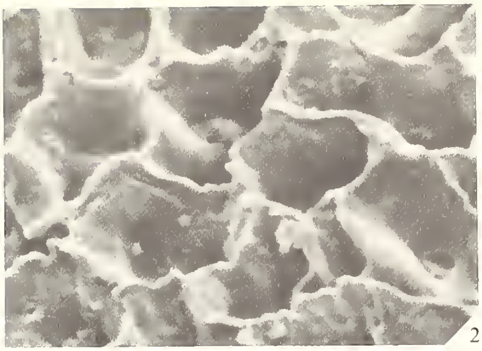
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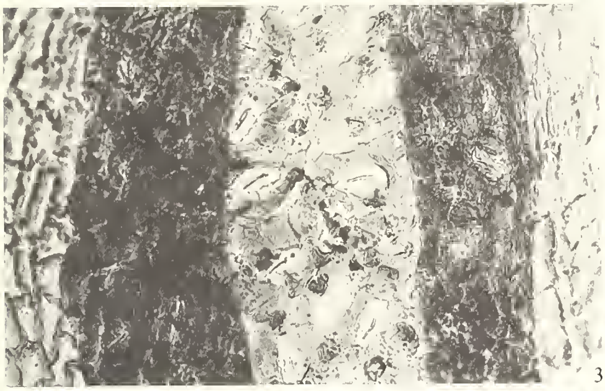
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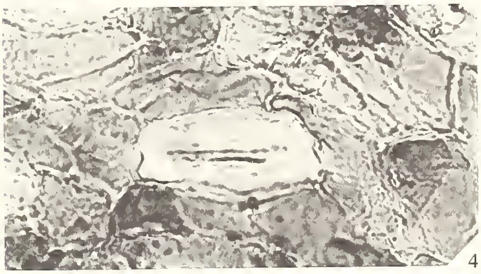
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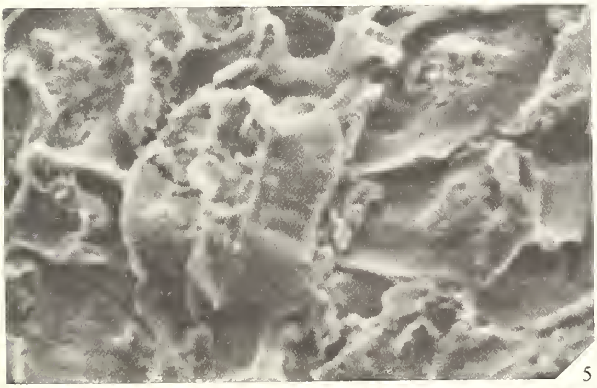
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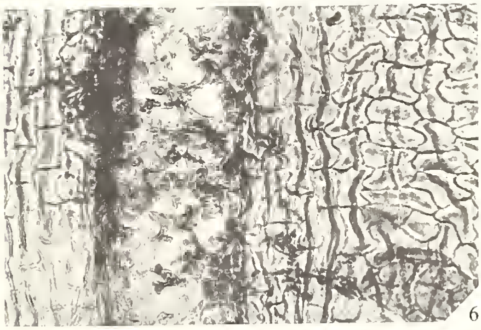
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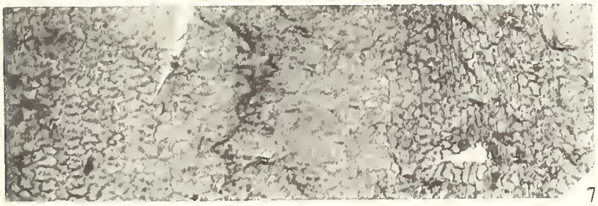
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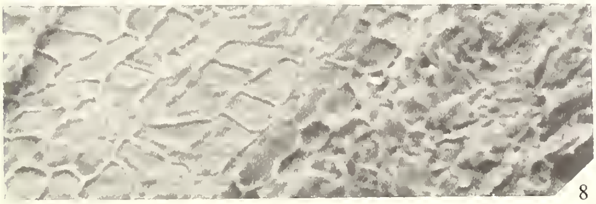
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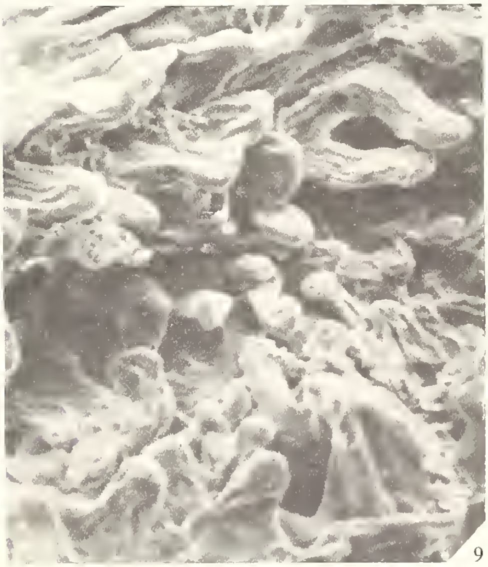
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OLDHAM, 11 cycad BeB and 12 cycad BeC

Cf. Genus ANOMOZAMITES Schimper
19 BENN AnA

Plate 65, figs. 1–5

Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material concentrated in laminae. Ten specimens, P98: 2/2.2; 12/3.2; 13/4.2; 15/1.2; 16/1.2, 2.1; 18/1.2, 4.2; 21/1.1; 23/1.2.

Systematic position. It is close to the genus *Anomozamites* Schimper and relates to Wealden species *A. lyellianus* (Dunker) Seward, although this species has transversely orientated stomata borne in regular rows. It also resembles *A. nilsonni* (Phillips) Harris, although again the arrangement of stomata is somewhat different.

Cf. Genus PTEROPHYLLUM Brongniart
20 BENN PtA

Plate 65, figs. 6–8

Record sample. Purbeck, Sample no. 53H. From 250-mm plant debris bed complex, medium-grey claystone, plant material in irregular laminae. Ten specimens, P95: 1/1.3; 5/1.1; 11/1.1, 4.2; 12/4.1; 16/1.2; 17/2.1, 4.1; 19/2.1, 3.1.

Systematic position. The almost straight walls of the epidermal cells suggest an affinity with *Pterophyllum* but none of the published members of that genus agree with this taxon.

21 BENN PtB

Plate 66, figs. 1–5

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 63/1.1, 2.2; 65/4.1; 66/2.1, 3.1.

Systematic position. Although bennettitalean in character it does not relate closely to any of the cuticles of Wealden leaves examined. Benda (1961) pictures a Bennettitee form 7, which resembles 21 BENN and Benda places his taxon in the genus *Pterophyllum.*

Cf. Genus CYCADOLEPIS Saporta
22 BENN CyA

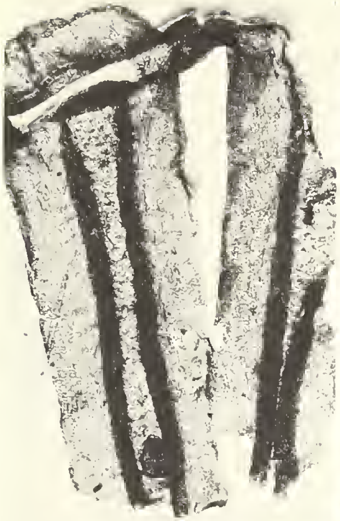
Plate 66, figs. 6–8

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band from plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 12/1.2, 3.1; 14/1.2; 15/3.2; 36/3.2.

EXPLANATION OF PLATE 62

Figs. 1–3. 13 BENN PeA. 1, ×20, LM., surface 2, general view; P49: 40/1.2. 2, ×2000, SEM., surface 2, inside, stoma; B63. 3, ×150, LM., surface 2, groove; P49: 40/1.2.

Figs. 4–7. 14 BENN PeB. 4, ×200, SEM., surface 2, outside, papillae; B57. 5, ×500, SEM., surface 2, inside, hypodermis; B57. 6, ×1000, SEM., surface 2, inside, stoma; B57. 7, ×500, SEM., surface 1, inside, epidermal cells; B57.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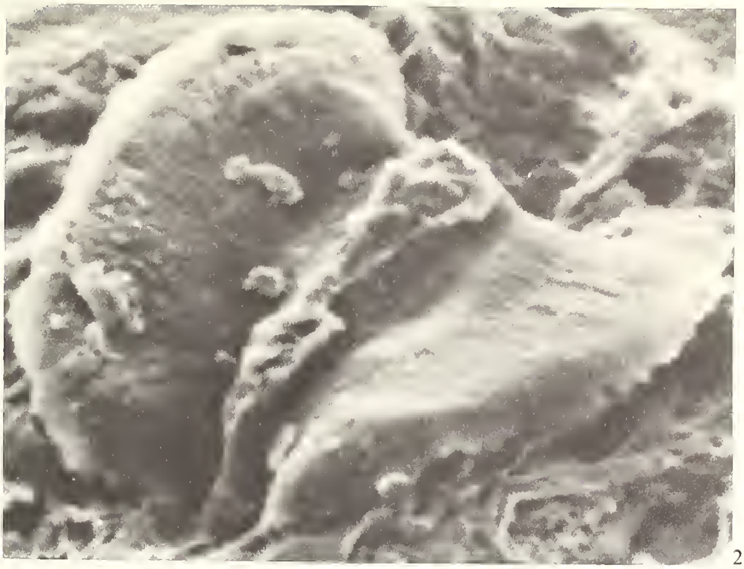
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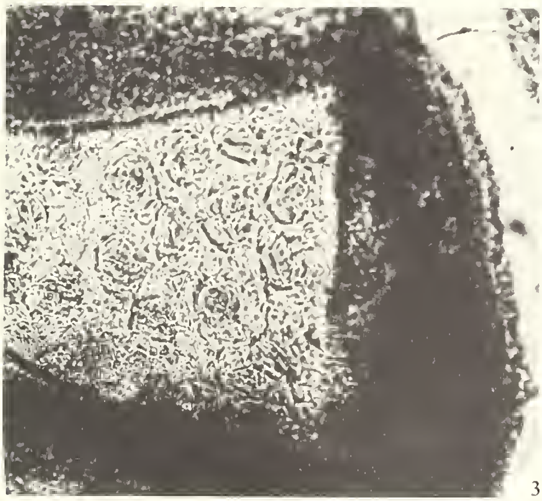
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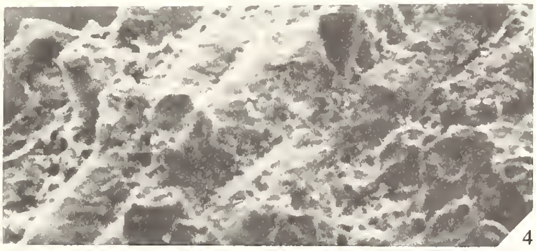
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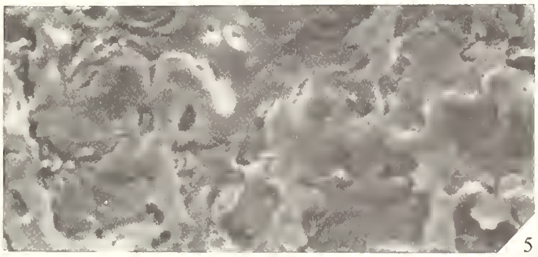
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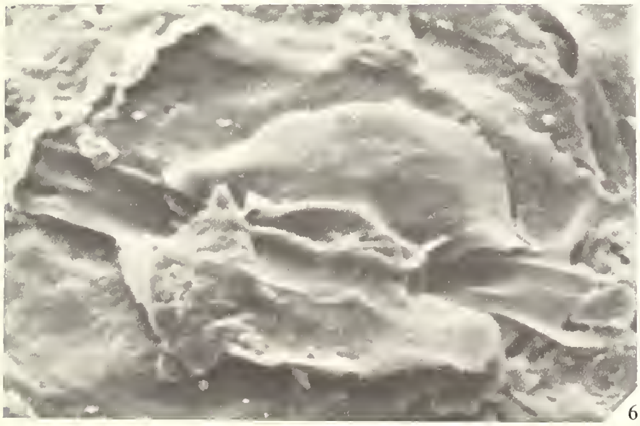
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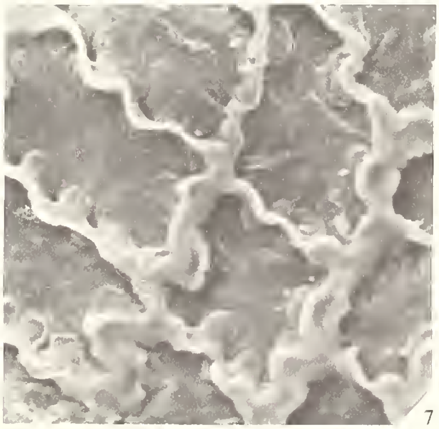
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OLDHAM, 13 BENN PeA and 14 BENN PeB

Systematic position. The stomata are bennettitalean in character and the straight walled epidermal cells and the scarcity of stomata suggest an affinity with *Cycadolepis* Saporta. Seward (1913) describes a *Cycadolepis* species from the English Wealden but the cuticle prepared from this is very poor. Daber's (1960) Blattfragment E is similar.

BENNETTITALES Incertae sedis
23 BENN BnA

Plate 67, figs. 1–8

Record sample. Wealden Marls, Sample no. 50CIOW. From 150-mm band from plant debris bed complex, medium light-grey siltstone, plant material in fine laminae. Five specimens, P153: 2/1.2; 3/3.1; 7/1.2, 3.2, 4.2.

Systematic position. It is bennettitalean in many of its characters but the stomata are not fully typical of the group.

Order GINKGOALES

Until Watson (1969) described *Pseudotorellia heterophylla*, no member of this order had been recorded from the English Wealden. The following six taxa relate to the Ginkgoales in varying degrees, but all fit in here better than with any other group.

Cf. Genus PSEUDOTORELLIA Florin
24 GINK ToB

Plate 68, figs. 1–3

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band from plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 9/1.2; 13/1.1; 19/3.2, 3.3; 24/4.1.

Systematic position. This taxon agrees with *P. heterophylla* Watson and an examination of the type material confirms this.

25 GINK ToA

Plate 68, figs. 4–8

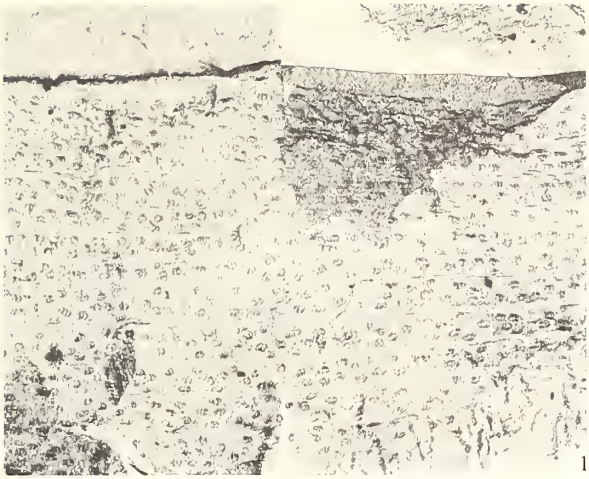
Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 9/1.1, 1.2, 2.1, 2.2; 16/1.2, 2.1, 3.2; 12/1.1; 45/1.1, 2.2.

Systematic position. This taxon agrees well with Watson's emended diagnosis of the genus *Pseudotorellia* (1969). Of the seven species described by Lundblad (1968)

EXPLANATION OF PLATE 63

Figs. 1–3. 15 BENN ZaA. 1, ×20, LM., surface 2, general view; P49: 14/1.1. 2, ×150, LM., surface 2, stomata; P49: 14/1.1. 3, ×500, LM., surface 2, stoma; P49: 13/2.2.

Figs. 4–7. 16 BENN ZaB. 4, ×20, LM., surface 2, general view; P49: 63/3.1. 5, ×1000, SEM., surface 2, outside, stomatal aperture; B62. 6, ×500, SEM., surface 2, inside, stoma, bordered holes; B62. 7, ×500, LM., surface 2, stoma; P49: 36/1.2.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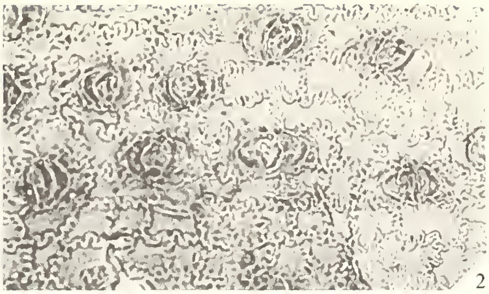
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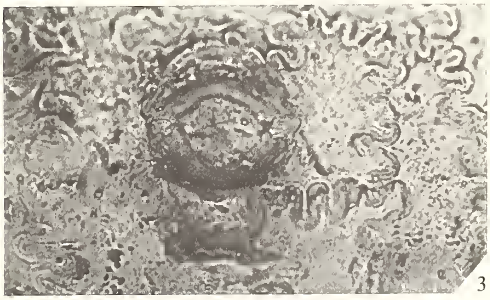
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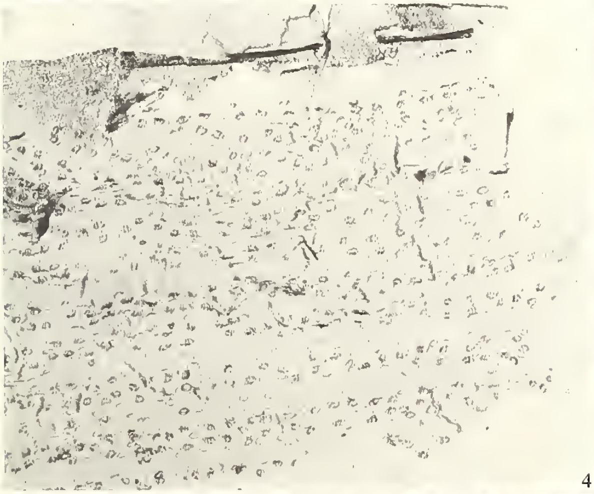
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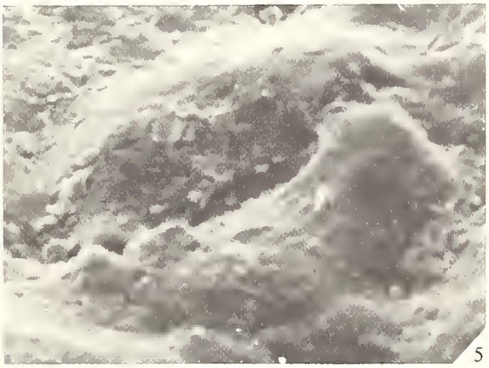
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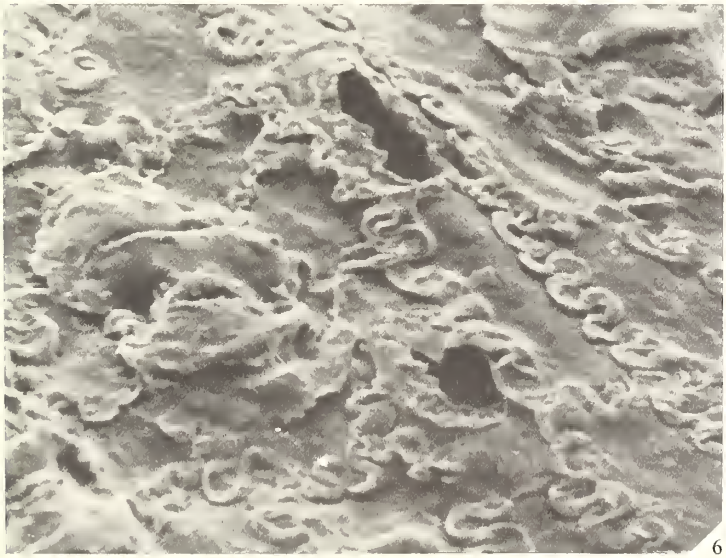
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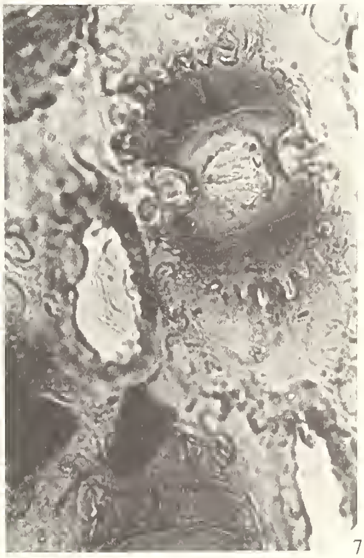
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OLDHAM, 15 BENN ZaA and 16 BENN ZaB

none agree completely with 25 GINK. It should be noted that specimens described as *Abietites linki* (Rom)Dunker by Michael (1936) and Benda (1961) appear to be identical with 25 GINK.

Cf. Genus GINKGOITES Seward
26 GINK GiA

Plate 69, figs. 1–6

Record sample. Wealden Marls, Sample no. 48CIOW. From 150-mm band from plant debris bed complex, medium light grey, fine siltstone, plant material in fine laminae. Five specimens, P147: 2/4.2; 4/4.2; 5/1.2; 6/2.2; 8/1.2.

Systematic position. It relates well to the ginkgoalean genera *Ginkgoites* Seward and *Baiera* Braun. It is not possible to distinguish these two genera apart on cuticle ground but the number of vein traces in the specimens of 26 GINK suggest a closer affinity to *Ginkgoites*. All the cuticle characters of these two genera that are described by Oishi (1933) are present in 26 GINK.

GINKGOALES Incertae sedis
27 GINK GkA

Plate 70, figs. 3–6; Plate 71, figs. 1, 3, 5

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 10/1.2, 2.1, 3.2; 11/1.2, 2.2, 2.1; 17/1.2, 2.2; 46/2.1.

Systematic position. This taxon is of ginkgoalean affinity but does not agree specifically with any of the published taxa.

28 GINK GkB

Plate 71, figs. 2, 4, 6, 7, 8

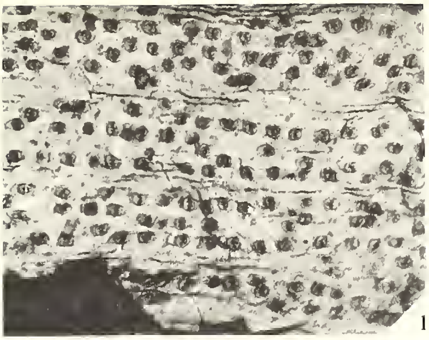
Record sample. Wealden Marls, Sample no. 20BD. From 300-mm plant debris bed complex, light grey, fine siltstone, plant material in irregular laminae. Five specimens, P121: 1/3.2; 2/1.1; 4/1.1; 6/1.1; 7/1.1.

Systematic position. It is closely related to 27 GINK and remarks made concerning the affinity of that taxon apply here.

EXPLANATION OF PLATE 64

Figs. 1–5. 17 BENN ZcC. 1, ×20, LM., surface 2, general view; P49: 63/2.1. 2, ×1000, SEM., surface 2, inside, stoma; B17. 3, ×2000, SEM., surface 2, inside, intracellular, circular, cutinized bodies; B17. 4, ×500, LM., surface 2, stomata and intracellular, circular, cutinized bodies; P49: 36/3.1. 5, ×150, LM., surface 1, epidermal cells; P49: 63/2.1.

Figs. 6–8. 18 BENN OtA. 6, ×150, LM., surface 2, stomata and papillae; P59: 37/4.2. 7, ×500, SEM., surface 2, inside, stoma; B16. 8, ×100, SEM., surface 2, outside, papillae; B16.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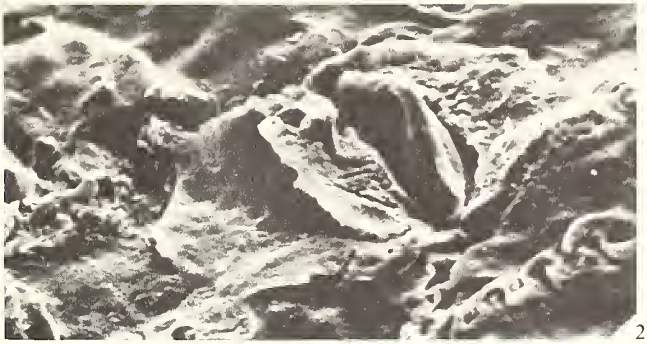
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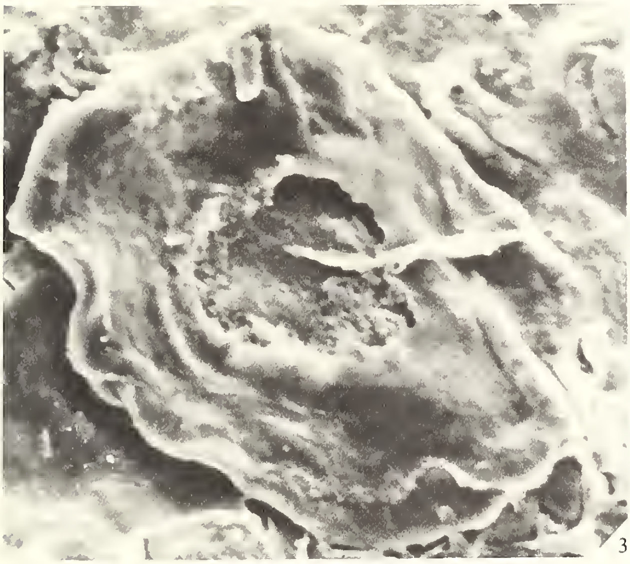
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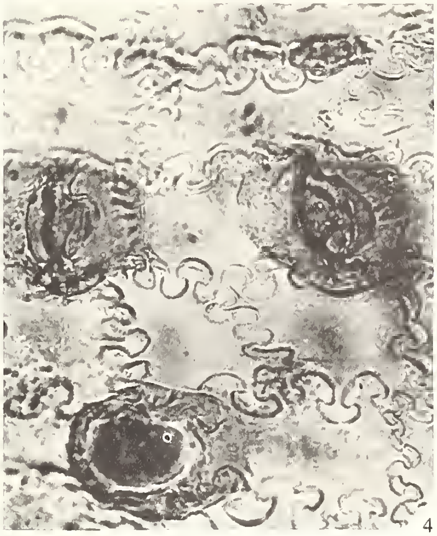
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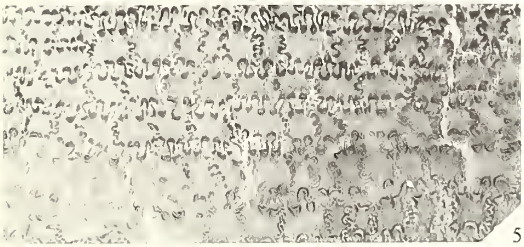
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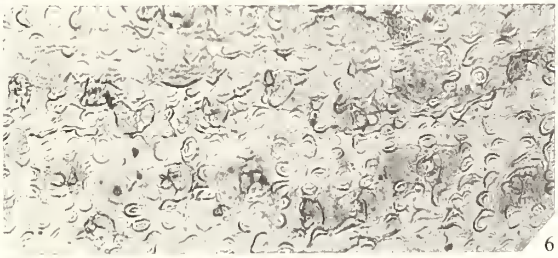
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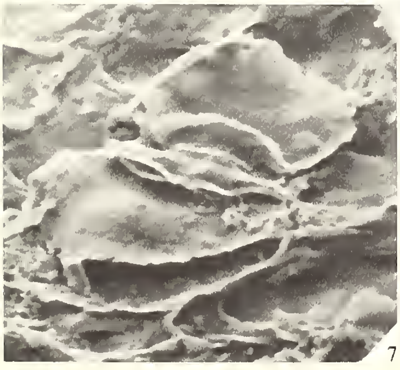
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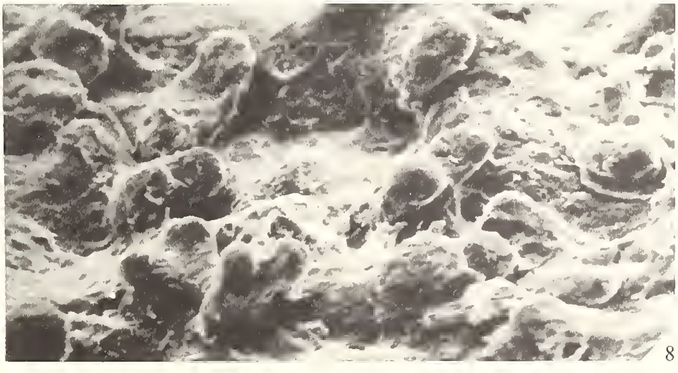
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OLDHAM, 17 BENN ZaC and 18 BENN OtA

29 GINK GkC

Plate 69, figs. 7, 8; Plate 70, figs. 1, 2

Record sample. Fairlight Clay, Sample no. P49. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 9/3.1; 12/1.2, 3.1, 3.2; 13/1.2, 3.1, 3.2; 14/2.1, 2.2; 21/3.

Systematic position. This is ginkgoalean in character and is close to the genera *Ginkgoites* and *Baiera*, although not agreeing sufficiently well to be placed in either genera.

Class CONIFEROPSIDA

Several species belonging to this class have been described from the English Wealden by Seward (1895, 1913) but many only relate to reproductive structures. In all he describes nine species that are defined by, or at least possess, leaves.

Order CONIFERAE

Family CHEIROLEPIDIACEAE Hirmer and Höurhammer emend. Takhtajan

30 CHEIR MaA

Plate 72, figs. 1-8

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 4/3.1, 4.1; 5/1.1, 2.1, 1.2; 6/1.1, 2.1, 2.2, 3.2, 4.2.

Systematic position. The cuticle structure resembles *Frenelopsis* but the phyllotaxis of 30 CHEIR is quite distinct. Its close association with *Classopollis* Pflug pollen in nearly every sample suggests an affinity with the family Cheirolepidiaceae. Archangelsky (1968) assigned this pollen grain to the family.

Family TAXODIACEAE

Cf. Genus SCIADOPITYTES Goeppert et Menge

31 TAXOD ScA

Plate 73, figs. 1-6

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Five specimens, P49: 40/1.1, 3.1; 53/1.1; 55/1.1; 57/1.2.

Systematic position. This taxon agrees well with Florin's (1922) diagnosis of the genus *Sciadopitytes*. It does not, however, agree in detail with any of the fourteen

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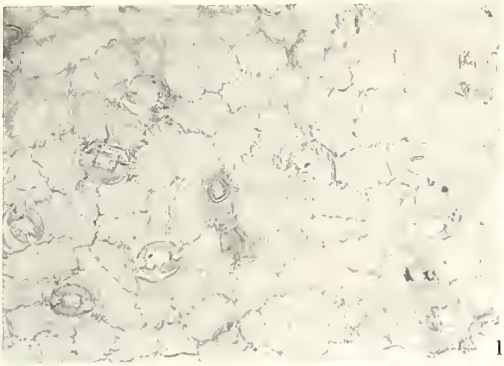
EXPLANATION OF PLATE 65

Figs. 1-5. 19 BENN AnA. 1, × 150, LM., surface 2, stomata; P98: 18/1.1. 2, × 500, SEM., surface 2, inside, stomata; B27. 3, × 2000, SEM., surface 2, inside, stoma; B27. 4, × 1000, SEM., surface 2, outside, hair base; B27. 5, × 1000, SEM., surface 2, outside, stomatal aperture; B27.

Figs. 6-8. 20 BENN PtA. 6, × 1000, SEM., surface 2, inside, stoma; B61. 7, × 500, SEM., surface 2, outside, ahir base; B61. 8, × 500, SEM., surface 2, outside, papillae, hair bases; B61.

PLATE 65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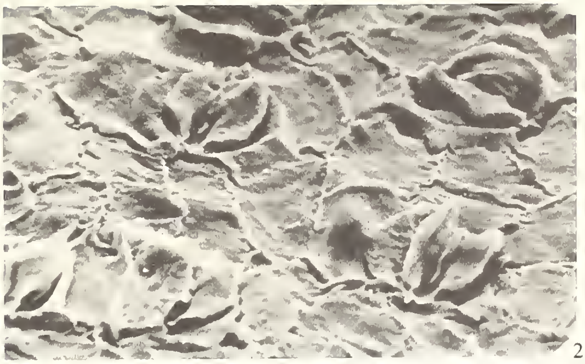
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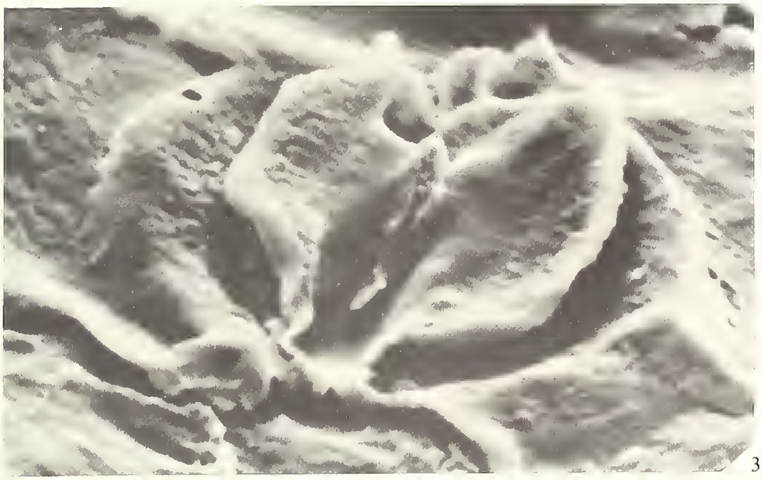
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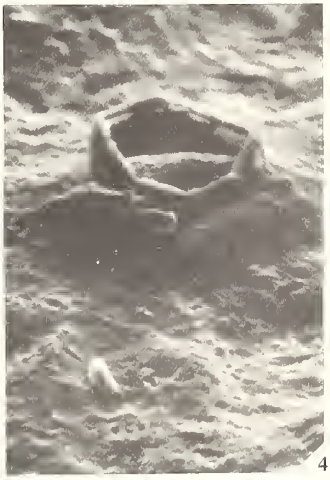
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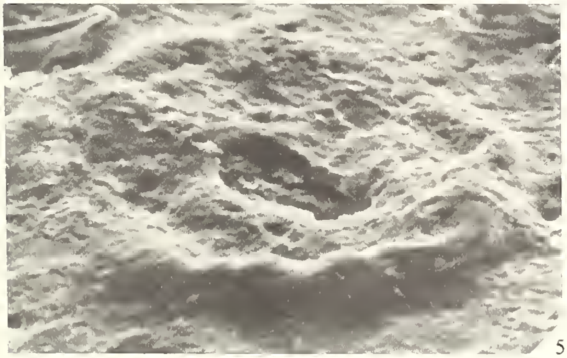
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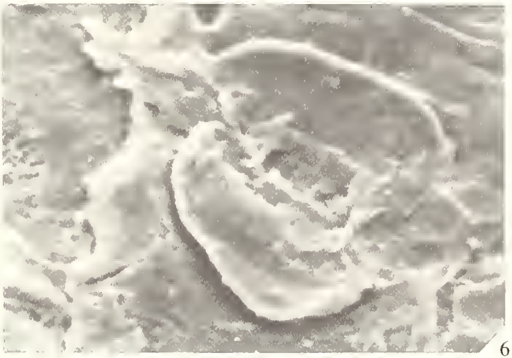
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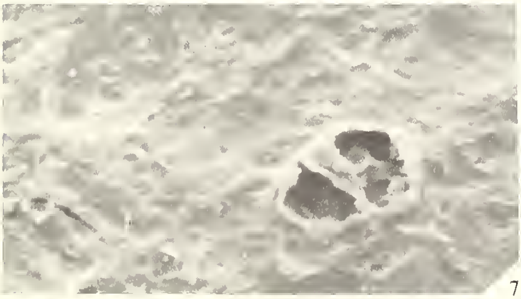
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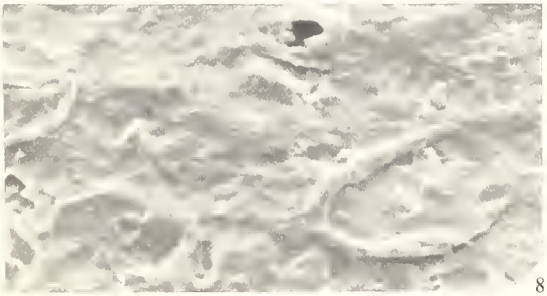
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OLDHAM, 19 benn AnA and 20 benn PtA

species he describes. It most resembles *S. macrophylla* but this species has no hairs along the stomatal groove and possesses a wider leaf. Gothan (1954) pictures a species of *Sciadopitytes* from the Wealden of Spain but his description is poor.

TAXODIACEAE Incertae sedis
32 TAXOD SpA

Plate 78, figs. 1–3

Record sample. Fairlight Clay, Sample no. 44H. From 50-mm band from plant debris bed complex, medium-grey siltstone, plant material in thick laminae. Ten specimens, P55: 5/4.1; 7/1.2, 2.2, 4.2; 9/3.2; 10/2.2, 3.2; 12/1.1, 1.2, 3.2.

Systematic position. The structure and arrangement of the stomata suggests a taxodiaceous affinity. It resembles the living genus *Athrotaxis* but the sinuous walled epidermal cells of 32 TAXOD are not a feature of this genus or indeed the family. Comparison with Mesozoic taxodiaceous genera shows this taxon to be distinct from most of them. It could be placed in *Sphenolepis* Schenk but this is a genus for leaves with a known cone, also the sinuous walls of the epidermal cells, the occasional sharing of subsidiary cells, and the presence of stomata on both surfaces are not characteristic of this genus. Similar arguments can be used against placing it in the genus *Elatides* Keer.

Family CUPRESSACEAE
Cf. Genus CUPRESSINOCLADUS Seward
33 CUPR CuA

Plate 74, figs. 1–7

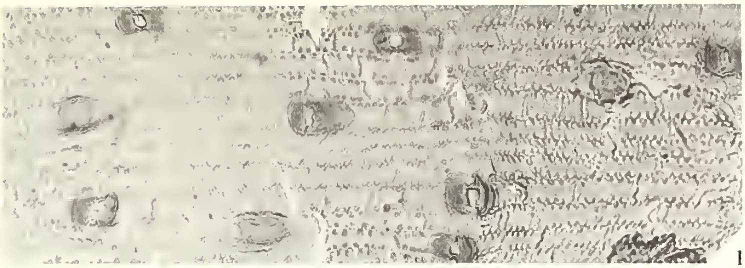
Record sample. Wealden Marls, Sample no. 3AD. From 300-mm plant debris bed complex, light grey, coarse siltstone, plant material concentrated in laminae. Ten specimens, P93: 5/1.1, 2.1, 3.1, 4.1, 1.2, 2.2; 8/2.1, 4.1, 2.2, 4.2.

Systematic position. The decussate arrangement of leaves in this taxon is reminiscent of the Cupressaceae. The genus *Cupressinocladus* was erected by Seward in 1919 for vegetative shoots showing such characters. This was slightly emended by Chaloner and Lorch (1960) and 33 CUPR agrees with the diagnosis. The several published species belonging to this genus agree in many respects with 33 CUPR but are all distinct in some features.

EXPLANATION OF PLATE 66

Figs. 1–5. 21 BENN PtB. 1, × 150, LM., surface 2, stomata; P49: 63/2.2. 2, × 500, LM., surface 2, stoma; P49: 63/2.2. 3, × 1000, SEM., surface 2, inside, intracellular, circular, cutinized bodies; B62. 4, × 500, SEM., surface 2, inside, epidermal cells; B62. 5, × 1000, SEM., surface 2, outside, stomatal aperture; B62.

Figs. 6–8. 22 BENN CyA. 6, × 20, LM., general view; P59: 12/3.1. 7, × 150, LM., stoma; P59: 12/3.1. 8, × 1000, SEM., inside, stoma; B45.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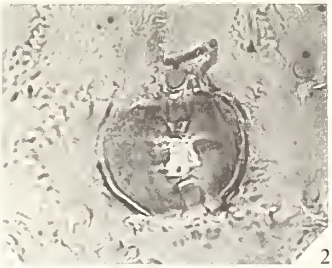
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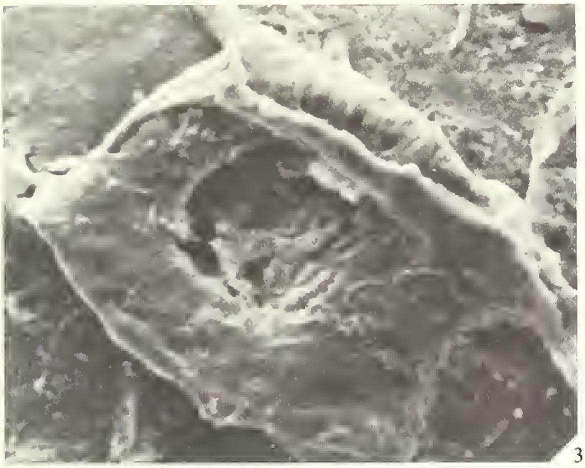
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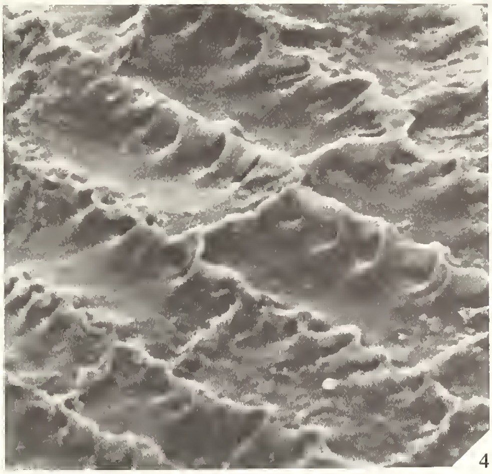
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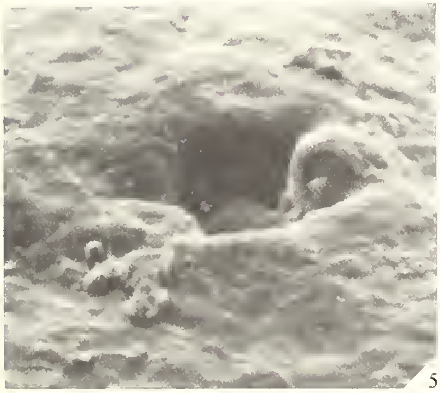
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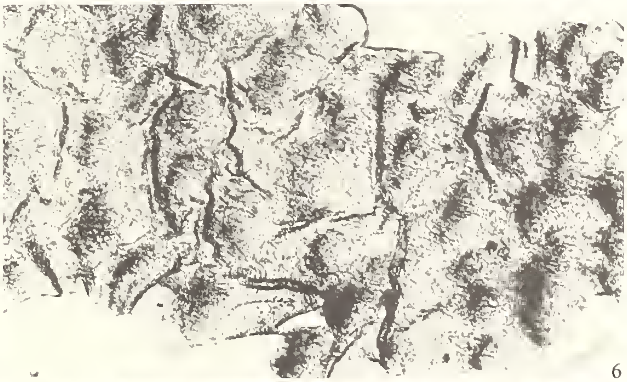
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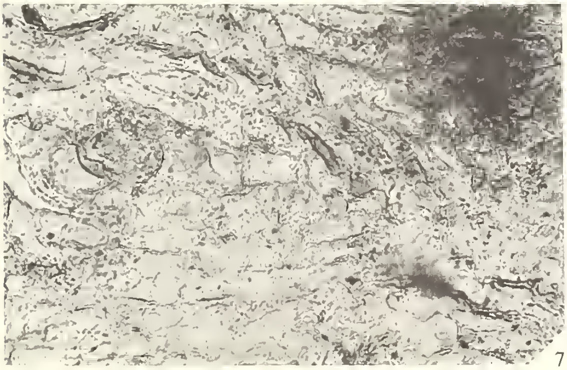
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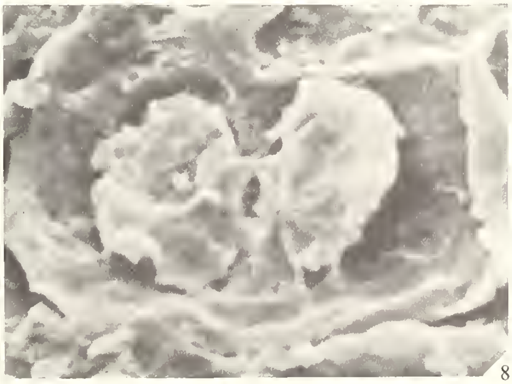
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OLDHAM, 21 BENN PtB and 22 BENN CyA

CONIFERAE Incertae sedis
Cf. Genus BRACHYPHYLLUM Brongniart
34 CONIF BrA

Plate 75, figs. 1–8

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Ten specimens, P59: 11/2.2; 31/1.1, 2.1, 1.3, 1.2, 2.2, 3.2; 32/1.1, 2.1, 2.2.

Systematic position. This taxon agrees with the diagnosis of this genus but does not agree specifically with any of the published taxa.

35 CONIF BrB

Plate 76, figs. 1–6

Record sample. Wealden Marls, Sample no. 7AD. From 25-mm band in plant debris bed complex, medium light-grey siltstone, plant material concentrated in laminae. Ten specimens, P101: 3/1.2, 2.2, 3.2; 4/4.1, 1.2; 5/2.1, 3.1, 4.1, 2.2, 3.2.

Systematic position. This is a leaf of the *Brachyphyllum* type but it does not agree with any of the published species. The combination of a frilled margin, papillate subsidiary cells, and papillate epidermal cells mark it off as a distinct new taxon.

36 CONIF BrC

Plate 77, figs. 1–7

Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material concentrated in laminae. Ten specimens, P98: 15/3.2, 4.1; 16/1.1; 17/1.1, 3.2; 18/2.1, 3.2; 20/2.2, 3.1; 21/2.2.

Systematic position. This resembles the cuticle that can be prepared from the specimens placed by Seward (1895) in *B. obesum* Heer. The preservation of the cuticle from Seward's specimens is poor, however, and will not allow an adequate comparison.

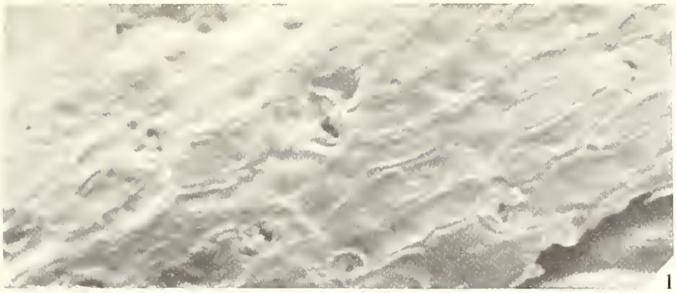
Class TAXOPSIDA
Order TAXALES
Cf. Genus TOMHARRISIA Florin
37 TAXAC ThA

Plate 78, figs. 4–8; Plate 79, fig. 1

Record sample. Wealden Marls, Sample no. 6D. From 300-mm plant debris bed complex, light-grey siltstone, plant material irregularly dispersed through the matrix. Ten specimens, P99: 2/3.1, 2.1; 5/1.2; 6/1.1, 1.2; 8/2.1; 9/1.2, 2.1; 10/2.2, 1.2.

EXPLANATION OF PLATE 67

Figs. 1–8. 23 BENN BnA. 1, ×200, SEM., outside, general view, hair bases; B60. 2, ×200, SEM., outside, general view, hair bases; B60. 3, ×1000, SEM., inside, stoma; B60. 4, ×1000, SEM., outside, hair base; B60. 5, ×500, SEM., inside, epidermal cells; B60. 6, ×1000, SEM., inside, epidermal cells and hypodermis; B60. 7, ×1000, SEM., outside, hair base; B60. 8, ×500, SEM., inside, epidermal cells; B60.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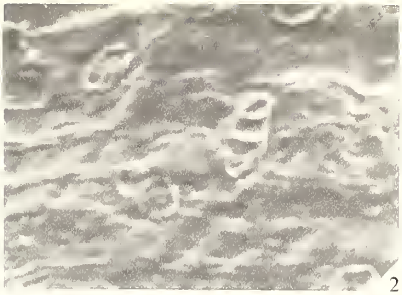
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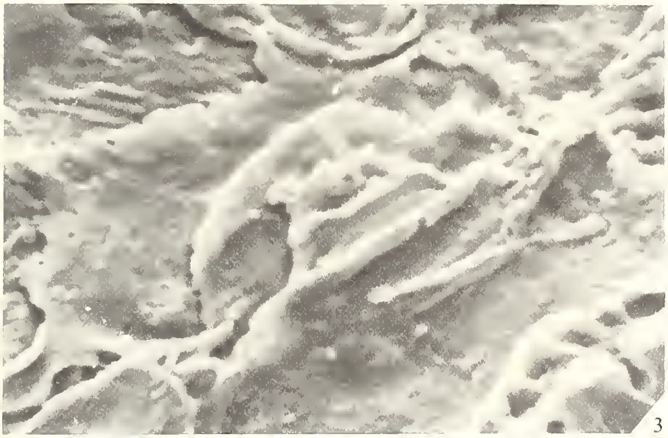
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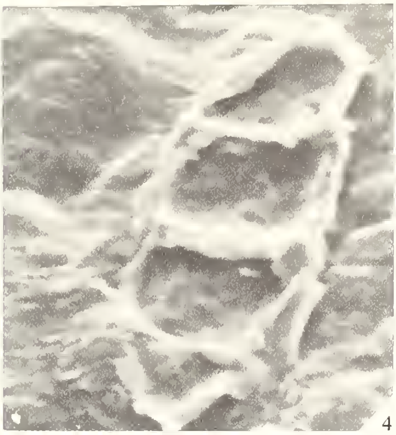
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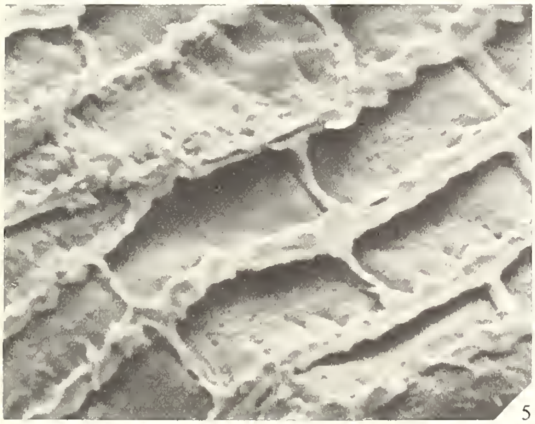
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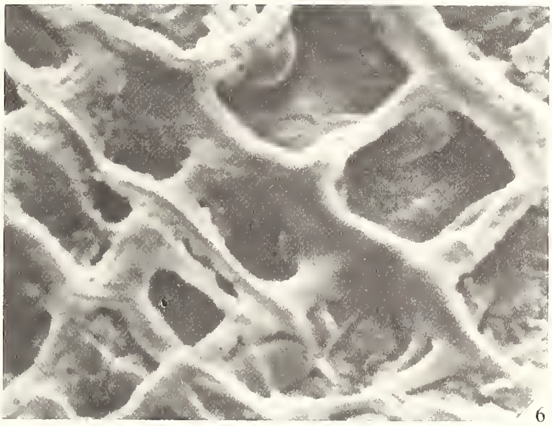
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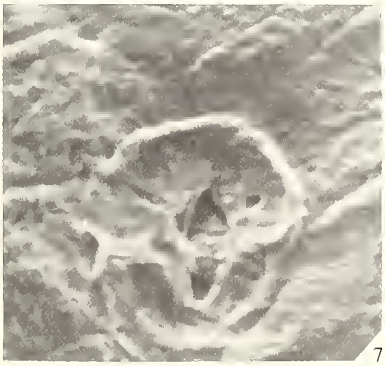
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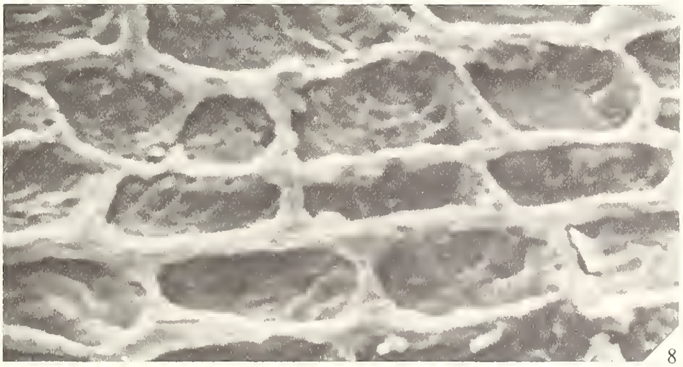
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OLDHAM, 23 BENN BnA

Systematic position. This taxon could belong in either the Coniferales or Taxales in terms of its cuticle characters. It does, however, resemble several Mesozoic genera that Florin (1958) relates to the Taxales. It is closest to *Tomharrisia* but does not agree completely with any of the published members of that genus.

GYMNOSPERMAE Incertae sedis

38 GYMN GyQ

Plate 79, figs. 2–4

Record sample. Fairlight Clay, Sample no. 51BH. From 600-mm plant debris bed complex, medium grey, fine siltstone, plant material in thick laminae. Ten specimens, P49: 18/2, 3; 27/1, 2, 3; 28/1, 2; 29/1, 2, 3.

Systematic position. This taxon does not appear to resemble any Mesozoic gymnosperm in its cuticle structure.

39 GYMN GyI

Plate 79, figs. 5–8

Record sample. Fairlight Clay, Sample no. 41H. From 50-mm band in plant debris bed complex, light-grey siltstone, plant material in irregular laminae. Five specimens, P59: 7/4.2; 14/3.2; 18/3.2; 33/3.2; 39/1.2.

Systematic position. This taxon does not appear to resemble any Mesozoic gymnosperm in its cuticle structure.

40 GYMN GyH

Plate 80, figs. 5–8

Record sample. Wealden Marls, Sample no. 20AD. From 300-mm plant debris bed complex, light grey, fine siltstone, plant material in fine laminae. Five specimens, P120: 1/2.1, 3.1; 6/1.1, 2.2, 3.2.

Systematic position. Little is known of the gross morphology of this taxon and the cuticle structure is unusual. It may relate to the cycadalean genus *Deltolepis* Harris but there is insufficient evidence to make a valid comparison.

41 GYMN GyD

Plate 80, figs. 1–4

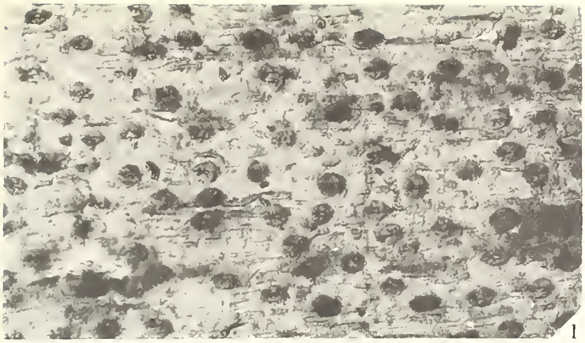
Record sample. Wealden Marls, Sample no. 5D. From 300-mm plant debris bed complex, light-grey siltstone, plant material in laminae. Ten specimens, P98: 6/4.2, 2.2; 13/3.1; 16/2.2, 4.2; 17/1.2, 2.2; 19/3.1; 20/2.1; 21/1.3.

Systematic position. This taxon is of uncertain affinity though it is possibly coniferalean.

EXPLANATION OF PLATE 68

Figs. 1–3. 24 GINK ToB. 1, ×50, LM., surface 2, general view; P59: 13/1.1. 2, ×500, LM., surface 2, stoma; P59: 13/1.1. 3, ×500, SEM., surface 2, inside, stoma; B44.

Figs. 4–8. 25 GINK ToA. 4, ×1000, SEM., surface 2, outside, stomatal aperture; B6. 5, ×20, LM., surface 2, general view; P49: 9/2.1. 6, ×20, LM., surface 2, general view; P49: 9/2.1. 7, ×1000, SEM., surface 2, inside, stoma; B6. 8, ×500, SEM., surface 2, inside, epidermal cells; B6.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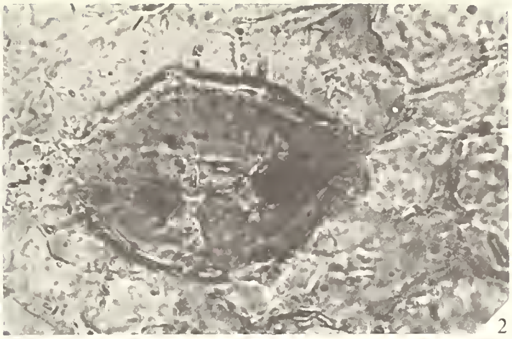
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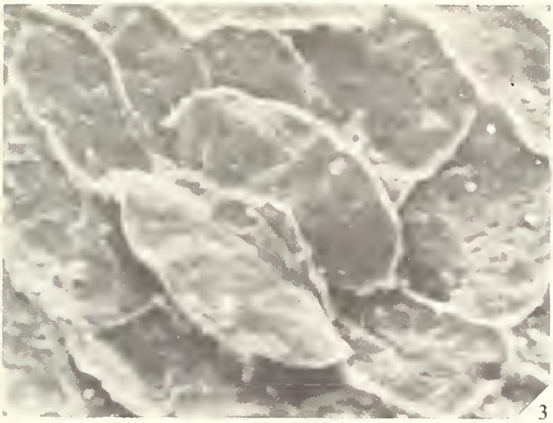
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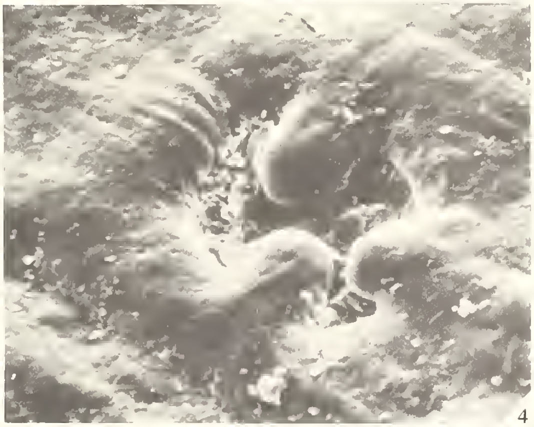
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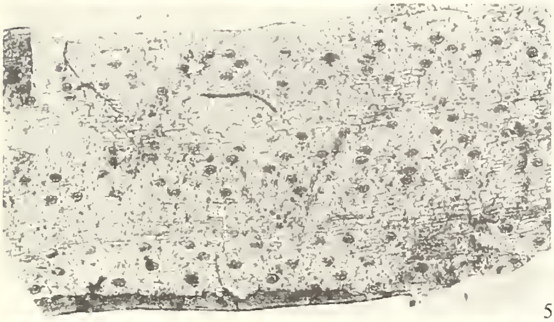
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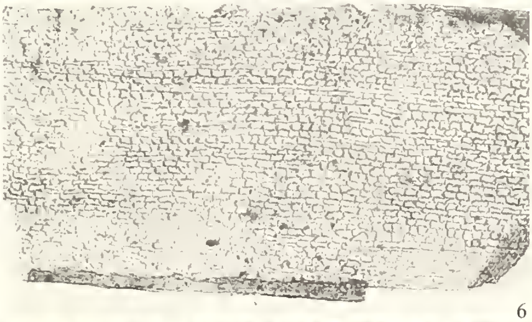
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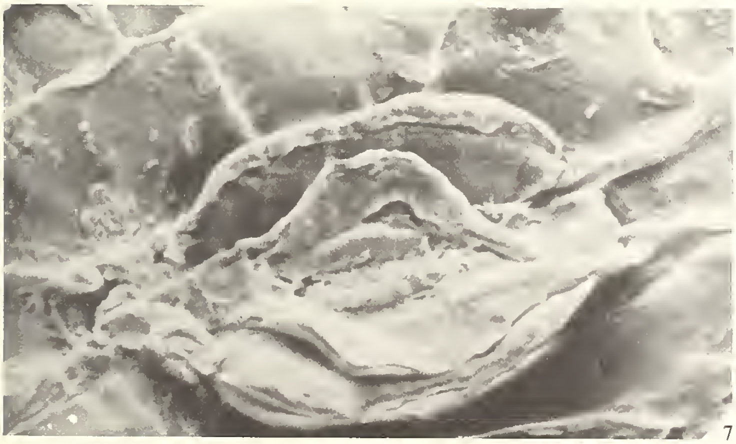
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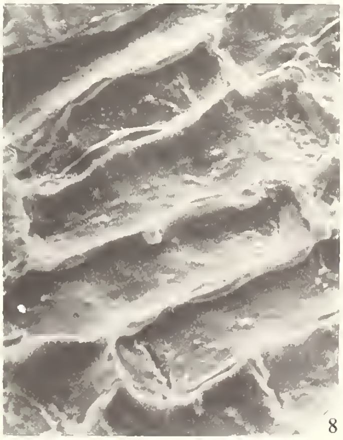
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OLDHAM, 24 GINK ToB and 25 GINK ToA

CLUSTER ANALYSIS OF DATA

A quantitative analysis of the contents of seventy-one samples from plant debris beds of the English Wealden is presented in Tables 1–3. These data were subjected to a cluster analysis following the methods of Bonham-Carter (1967). The resulting

TABLE 1. Analysis of the content of samples from the Isle of Wight succession.

	40IOW	39IOW	41IOW	42BIOW	43IOW	44IOW	47IOW	48DIOW	48CIOW	48AIOW	49AIOW	49BIOW	50EIOW	50DIOW	50CIOW	50BIOW	50AIOW
3 CYCAD	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	–
4 CYCAD	3	3	–	–	–	–	3	–	3	–	–	–	3	3	3	3	3
6 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	2	2	3	2	–
8 CYCAD	–	–	–	–	–	2	–	2	2	2	–	–	2	2	2	2	2
12 CYCAD	–	–	–	–	–	2	–	–	2	2	–	–	–	–	–	–	3
13 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2	–
14 BENN	–	–	–	–	–	2	–	–	–	–	–	–	2	–	2	2	–
16 BENN	–	–	–	–	–	–	–	–	–	2	–	2	–	2	–	2	–
17 BENN	–	–	–	2	–	2	–	–	2	3	2	–	3	3	3	3	3
18 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	3	3	3	–
19 BENN	–	–	–	–	–	–	–	2	2	–	2	–	3	2	3	2	3
21 BENN	–	–	–	–	–	–	–	2	2	–	2	–	–	–	–	–	–
22 BENN	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–
23 BENN	–	–	–	–	–	–	–	–	2	2	–	3	3	3	3	3	3
25 GINK	3	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26 GINK	–	2	–	–	–	2	–	2	2	–	2	–	–	–	–	–	3
28 GINK	2	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
29 GINK	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
30 CHEIR	4	3	–	–	–	–	2	–	–	2	5	5	1	1	2	–	–
32 TAXOD	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–
36 CONIF	4	4	3	4	4	5	–	5	5	5	4	3	4	4	4	3	5
37 TAXAC	2	2	–	–	2	2	–	–	2	–	–	–	2	2	2	2	2
40 GYMN	–	–	–	2	–	2	–	–	–	–	–	–	–	–	–	–	–
41 GYMN	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–
WOOD Bl	3	3	5	4	3	3	5	3	3	3	4	2	4	4	4	4	4
WOOD Br	4	4	3	3	5	3	2	2	3	2	5	2	3	3	3	4	3
MEGASPR	1	1	1	2	2	3	–	2	2	1	1	1	2	3	3	3	2
SEEDS	3	2	1	2	2	3	2	2	2	2	2	2	3	3	3	3	2

All plant material present in the samples is scored on a five-point abundance scale. 1 = rare, 2 = occasional, 3 = frequent, 4 = abundant, 5 = very abundant.

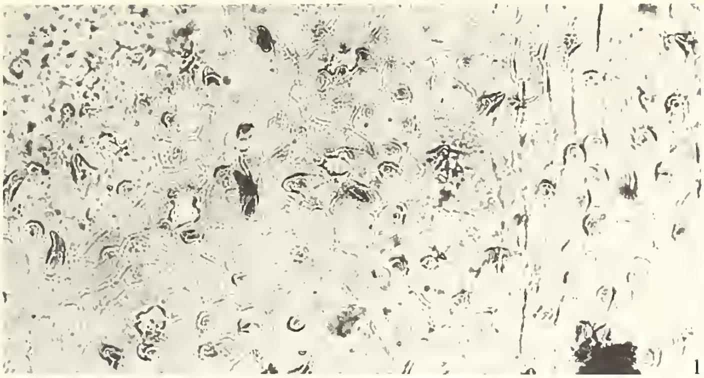
Abreviations used: WOOD Bl = Black wood, WOOD Br = Brown wood, MEGASPR = Megaspores.

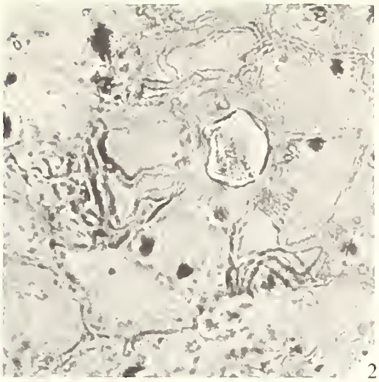
Samples are arranged in ascending stratigraphic order from left to right.

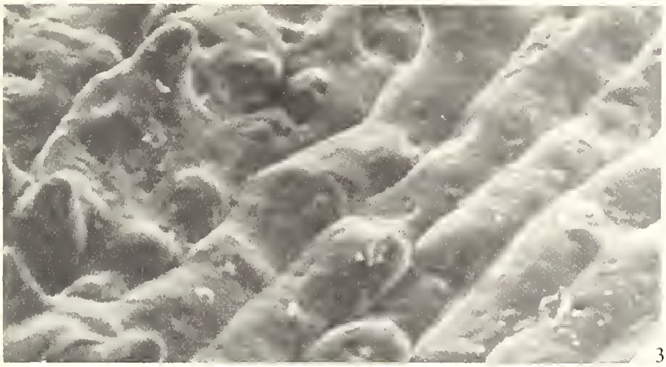
EXPLANATION OF PLATE 69

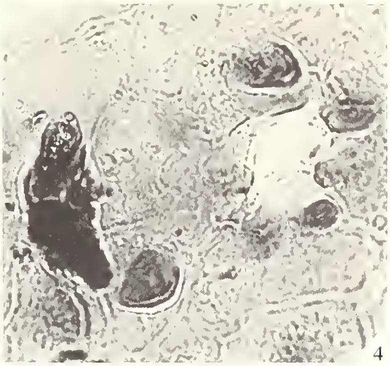
Figs. 1–6. 26 GINK GiA. 1, × 150, LM., surface 2, general view; P147: 2/4.2. 2, × 500, LM., surface 1, stoma; P147: 2/4.2. 3, × 500, SEM., surface 2, outside, stomatal aperture, papillae; B66. 4, × 500, LM., surface 2, stoma; P147: 2/4.2. 5, × 1000, SEM., surface 2, inside, epidermal cells; B66. 6, × 1000, SEM., surface 2, inside, stoma; B66.

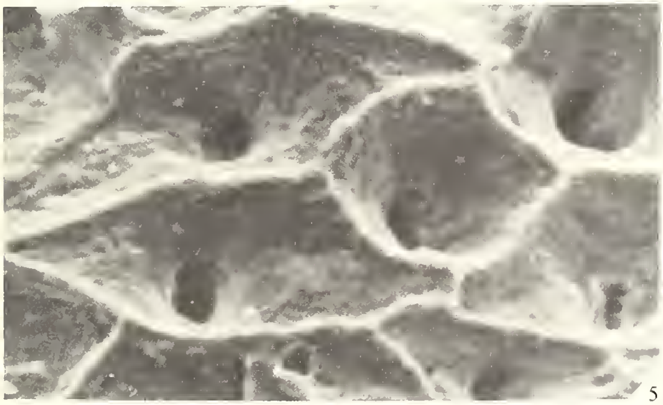
Figs. 7, 8. 29 GINK GkC. 7, × 150, LM., surface 2, general view; P49: 9/3.1. 8, × 500, LM., surface 2, stoma; P49: 9/3.1.

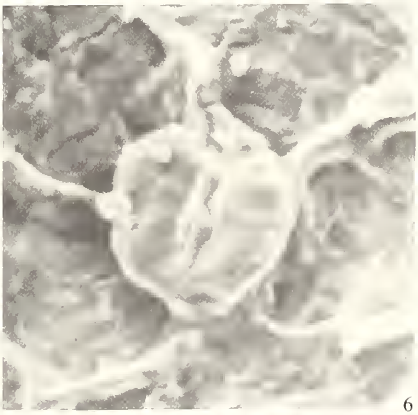


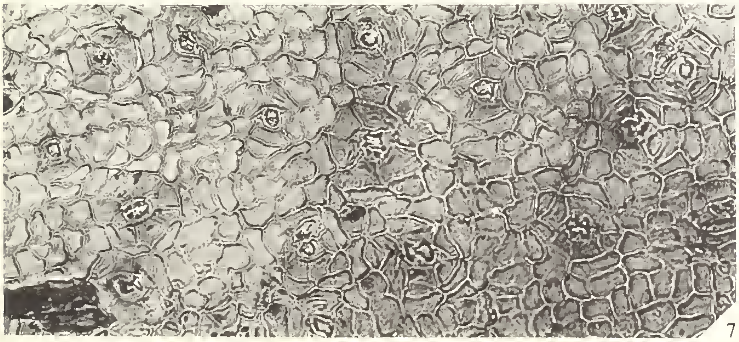


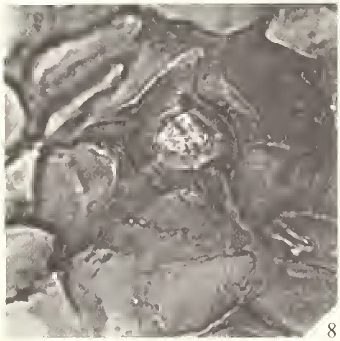












OLDHAM, 26 GINK GiA and 29 GINK Gkc

TABLE 2. Analysis of the content of samples from the Dorset succession. See Table 1 for key to abundance scale.

	SWANAGE BAY									WORBARROW BAY															
	8D	7AD	7BD	7DD	6D	5D	3BD	3AD	2AD	22D	20BD	20AD	18DD	18CD	18BD	18AD	17D	27DD	27CD	27BD	27AD	13D	11BD	11AD	10D
1 CAYT	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
3 CYCAD	2	2	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	3	–	3	–	–	–	–	–
4 CYCAD	3	–	3	2	2	2	–	–	3	–	2	3	2	–	2	2	–	–	–	–	–	–	–	–	–
5 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–
6 CYCAD	–	–	2	2	2	–	–	–	2	–	2	–	–	–	–	–	–	–	2	–	–	–	–	–	–
8 CYCAD	–	–	–	–	2	2	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	2	1
9 CYCAD	2	2	2	2	–	2	–	–	–	–	–	2	2	–	3	2	–	–	–	–	–	–	2	–	3
12 CYCAD	2	–	4	3	–	3	–	–	–	–	3	2	3	2	–	–	–	–	–	–	–	–	2	3	–
13 BENN	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16 BENN	2	–	–	2	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
17 BENN	3	–	3	–	2	–	–	–	3	–	3	3	–	–	–	–	–	–	2	–	–	2	–	–	3
18 BENN	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
19 BENN	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2
21 BENN	2	–	–	2	–	–	–	–	2	–	–	2	2	–	2	–	–	–	2	2	2	–	–	–	2
22 BENN	2	–	2	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
23 BENN	–	–	–	–	–	2	–	2	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	3
25 GINK	2	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
26 GINK	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
27 GINK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–
28 GINK	–	–	–	2	–	–	–	–	–	–	3	3	–	–	2	2	–	–	–	–	–	–	–	–	–
29 GINK	–	–	–	2	2	2	–	–	–	–	–	–	–	–	2	–	–	–	–	2	–	3	2	3	2
30 CHEIR	4	4	4	4	4	2	–	2	–	4	3	4	5	5	5	5	5	5	5	5	5	5	5	5	–
31 TAXOD	–	–	–	–	–	–	–	–	–	–	4	2	2	–	–	–	–	–	–	–	–	–	–	–	–
33 CUPR	–	–	–	–	–	4	5	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
34 CONIF	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35 CONIF	3	4	3	2	3	–	–	–	–	–	–	2	–	–	–	–	2	–	1	1	1	–	3	–	–
36 CONIF	4	2	2	3	–	4	2	1	3	–	3	3	2	–	–	–	2	–	–	–	–	2	3	2	4
37 TAXAC	2	2	2	2	3	2	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
40 GYMN	–	–	–	–	–	2	–	–	–	–	2	3	2	–	2	–	–	–	–	–	–	–	–	–	–
41 GYMN	2	–	–	–	2	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
WOOD Bl	1	1	2	1	2	2	–	–	4	2	2	2	3	2	1	2	3	3	3	3	3	2	2	2	4
WOOD Br	3	4	3	3	4	3	3	3	2	5	3	3	4	4	4	4	4	4	3	3	3	4	4	3	2
MEGASPR	2	–	2	2	2	–	–	–	3	2	3	4	3	2	2	2	–	–	–	–	–	2	2	2	1
SEEDS	1	1	1	2	2	2	–	1	2	–	2	2	2	2	2	2	1	–	2	–	2	2	2	2	2

dendrograms (deposited with the British Library) were examined for meaningful associations. No single factor was found to explain all the groups but stratigraphic proximity, geographical location, and the cuticle species richness of the samples were all important.

Comparison of the samples on the basis of their total cuticle assemblage did not bring about an ordering of them in a precise stratigraphic fashion. This is best explained by the fact that so many of the samples contained so few species they

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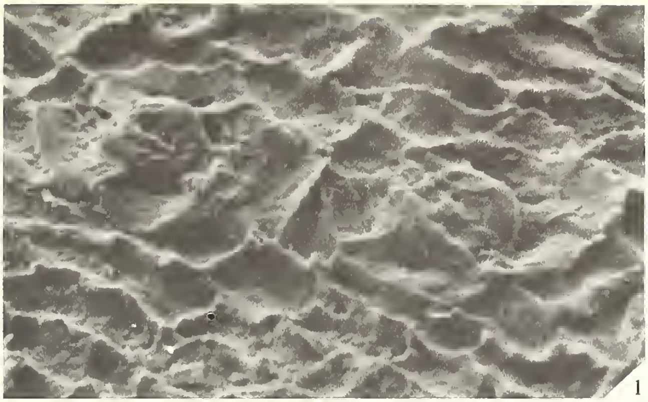
EXPLANATION OF PLATE 70

Figs. 1, 2. 29 GINK GkC. 1, ×500, SEM., surface 2, inside, stomata; B40. 2, ×200, SEM., surface 2, outside, stomatal apertures; B40.

Figs. 3–6. 27 GINK GkA. 3, ×50, LM., surface 2, general view; P49: 10/2.1. 4, ×500, LM., surface 2, stomata; P49: 10/2.1. 5, ×1000, SEM., surface 2, inside, stoma; B39. 6, ×200, SEM., surface 2, inside, groove and non stomatal area; B39.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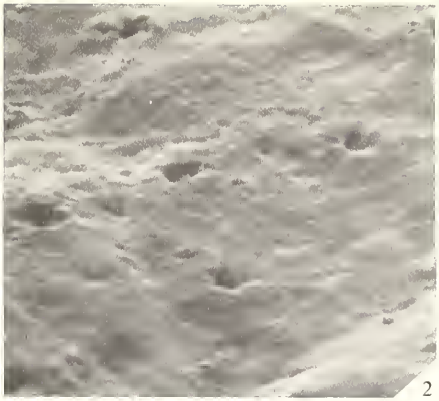
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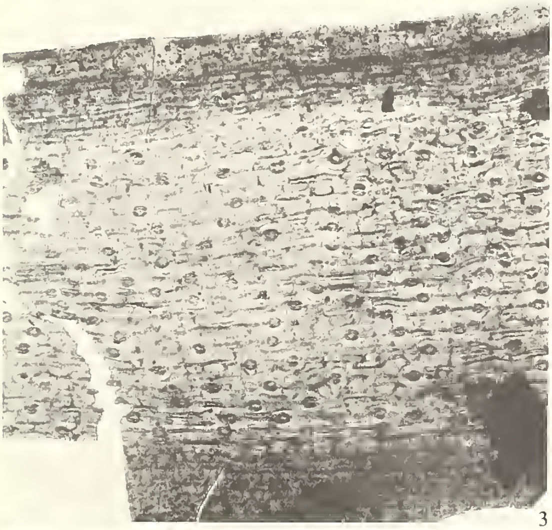
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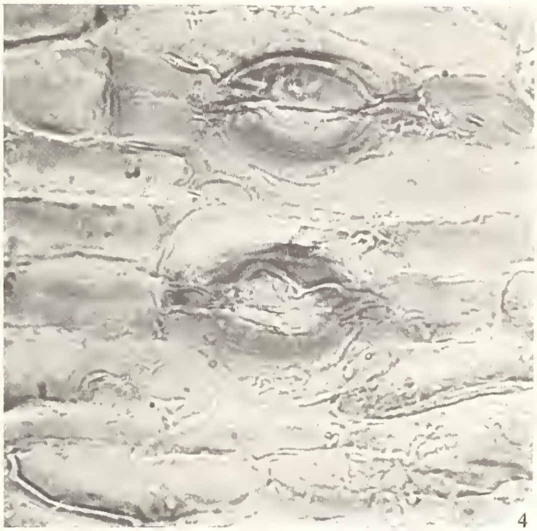
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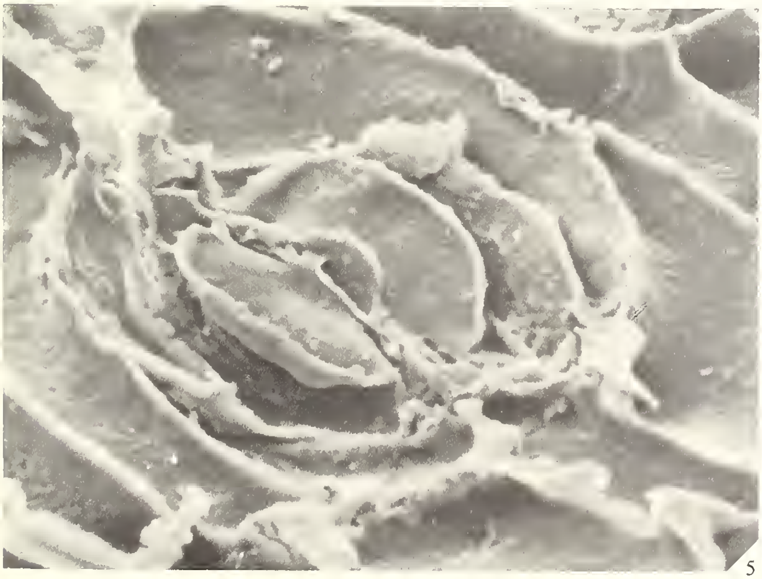
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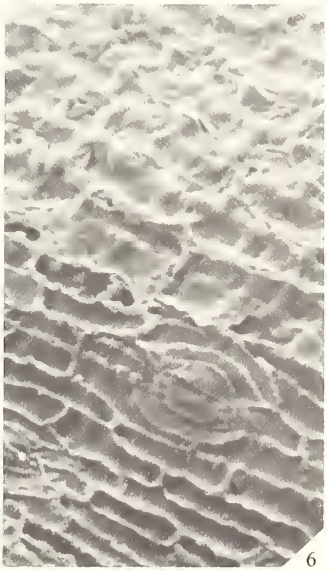

6

OLDHAM, 29 GINK Gkc and 27 GINK GkA

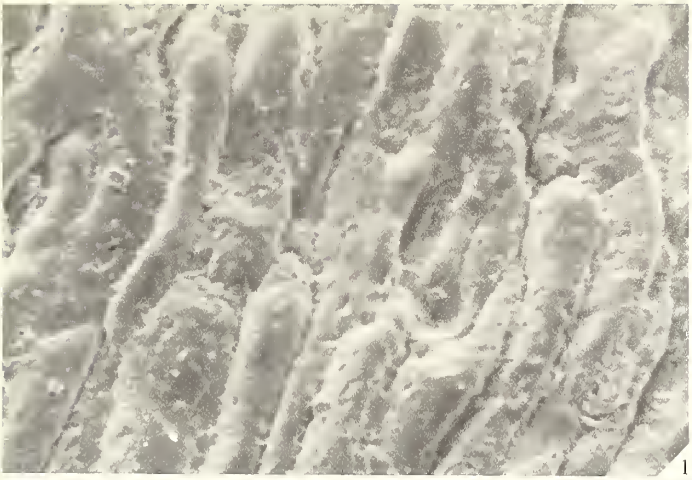
TABLE 3. Analysis of the content of samples from the South-eastern succession. See Table 1 for key to abundance scale.

	53H	21BH	19H	22H	18AH	25H	26H	27H	28H	30H	32H	33H	23H	13H	41H	34AH	44H	51BH	15AH	7AH	14H	47H	CUC931	54H	CUC635	CUC634	CUC443	CUC434	CUC431
1 CYAT	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	4	1	–	–	–	–	–	–	–	–
2 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–
3 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	2	3	–	–	–	–	–	–	–	–	–
4 CYCAD	3	–	–	3	4	–	2	–	–	–	–	–	–	4	3	–	–	3	3	–	2	2	–	3	–	–	–	2	–
6 CYCAD	–	–	2	2	3	–	–	–	–	–	2	2	–	3	2	–	2	–	2	–	–	–	–	–	2	2	–	–	–
7 CYCAD	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8 CYCAD	–	–	–	2	–	–	–	–	–	–	2	–	–	2	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
10 CYCAD	–	–	–	–	2	–	–	–	–	–	–	–	–	2	–	–	–	3	–	–	–	–	–	–	–	–	–	2	2
11 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	2	2
13 BENN	–	–	–	–	3	–	–	–	–	–	–	–	–	3	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
14 BENN	–	–	–	–	2	–	–	–	–	–	–	–	–	–	2	4	–	–	–	–	–	–	–	–	–	–	–	–	–
15 BENN	–	–	–	2	3	–	–	2	–	–	–	–	–	4	4	–	–	3	–	–	–	–	–	–	–	–	–	–	–
16 BENN	–	–	–	2	3	–	–	–	–	–	2	–	2	3	3	–	–	3	2	–	–	–	–	–	–	2	–	–	–
17 BENN	–	–	–	3	4	–	–	–	–	–	2	–	2	3	3	–	–	3	–	–	–	2	–	–	3	3	–	3	3
18 BENN	–	2	–	3	3	–	–	–	–	2	–	–	–	3	3	–	–	–	–	–	2	–	–	2	–	–	–	–	–
19 BENN	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20 BENN	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
21 BENN	–	–	–	–	2	–	–	–	–	–	–	–	–	2	–	–	–	3	2	2	–	–	–	–	–	–	–	–	2
22 BENN	–	–	–	3	–	–	–	–	–	–	–	–	3	3	3	–	–	3	–	–	–	–	–	–	–	–	–	–	–
23 BENN	–	–	2	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
24 BENN	–	–	–	–	2	–	–	–	–	–	–	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
25 GINK	–	–	–	–	3	–	–	–	–	–	–	3	–	3	2	–	–	3	–	–	–	–	2	–	–	–	–	–	–
27 GINK	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	4	–	–	–	–	–	–	–	–	–	–	2
28 GINK	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
29 GINK	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–
30 CHEIR	2	2	2	–	2	–	–	–	–	2	2	–	2	2	–	–	–	5	–	–	3	–	–	–	4	4	2	3	4
31 TAXOD	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
32 TAXOD	–	–	–	2	–	–	–	2	–	–	–	–	–	–	–	–	5	–	–	–	–	–	2	3	–	–	–	–	–
34 CONIF	4	4	4	4	4	4	3	–	4	3	3	–	3	3	3	2	2	–	–	–	3	–	–	–	2	–	–	–	–
35 CONIF	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–
36 CONIF	3	3	4	4	3	4	3	4	4	4	4	3	–	4	2	4	2	4	3	3	3	3	–	–	4	3	4	4	4
38 GYMN	–	–	–	2	2	–	–	–	–	–	–	–	–	3	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–
39 GYMN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
40 GYMN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
WOOD Bl	1	4	3	3	3	4	3	4	3	4	3	2	1	2	2	3	4	2	3	3	2	5	4	5	3	3	3	4	3
WOOD Br	2	3	3	2	3	3	4	3	3	4	3	4	1	2	–	–	–	1	4	3	–	2	2	3	2	3	2	3	3
MEGASPR	–	3	1	2	–	1	3	1	1	2	2	2	1	1	–	1	1	–	4	3	5	4	3	4	2	3	4	3	3
SEEDS	2	3	2	2	1	2	2	1	2	2	2	2	1	2	2	2	2	1	2	3	2	1	1	2	2	2	2	2	2

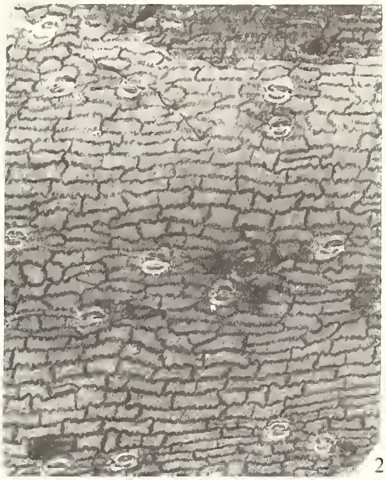
EXPLANATION OF PLATE 71

Figs. 1, 3, and 5. 27 GINK GkA. 1, ×500, SEM., surface 2, outside, ridges and stomatal apertures; B39. 3, ×150, LM., surface 1, epidermal cells and hypodermis; P49: 10/2.1. 5, ×500, SEM., surface 1, inside, epidermal cells and hypodermis; B39.

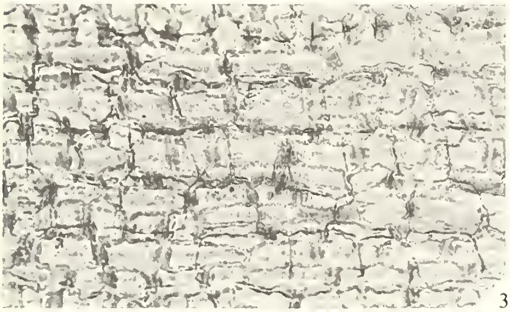
Figs. 2, 4, 6–8. 28 GINK GkB. 2, ×50, LM., surface 2, general view; P121: 2/1.1. 4, ×150, LM., surface 1, epidermal cells; P121: 2/1.1. 6, ×500, SEM., surface 2, inside, epidermal cells; B25. 7, ×500, SEM., surface 2, outside, stomatal apertures; B25. 8, ×1000, SEM., inside, stoma; B25.



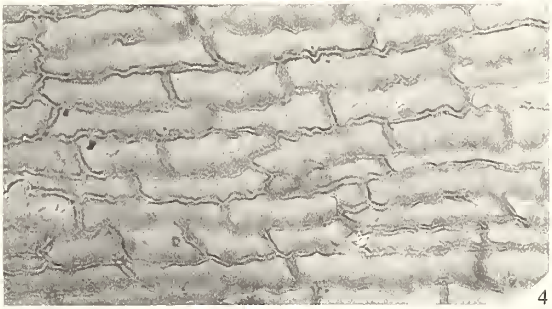
1



2



3



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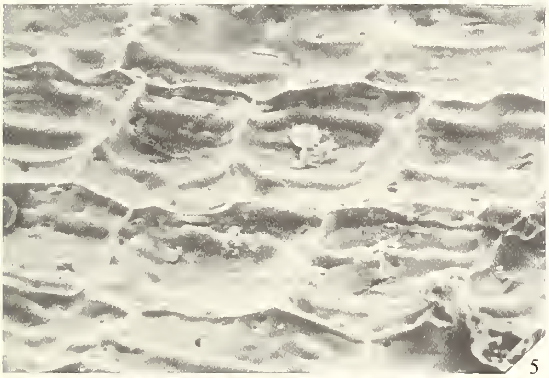

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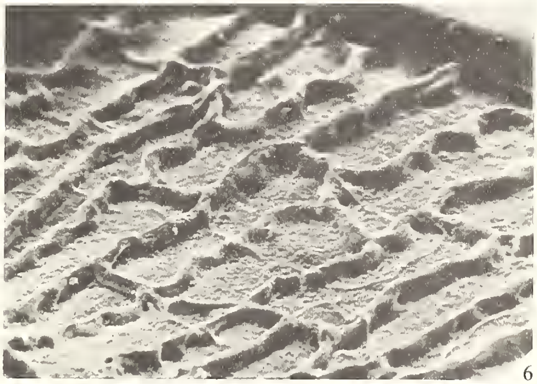

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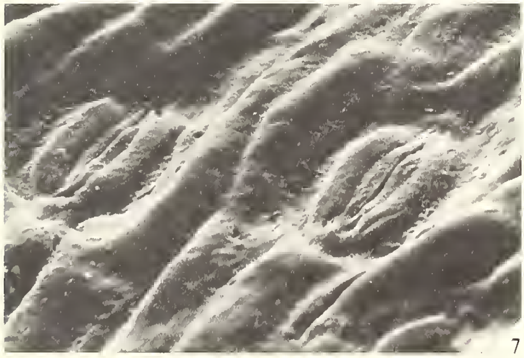

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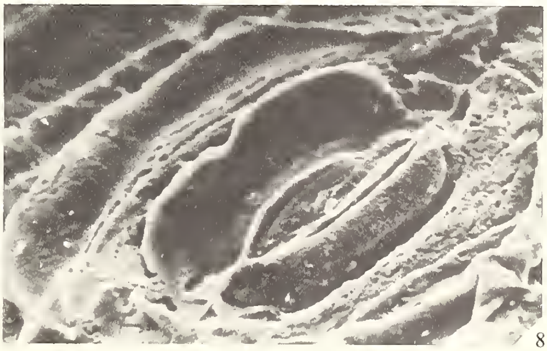


8

OLDHAM, 27 GINK GkA and 28 GINK GkB

masked any trend. Indeed, the lack of sites from which good cuticular material can be obtained in the English Wealden is a serious drawback to any quantitative study.

This aside, certain significant groupings were shown by the clustering procedure:

1. The samples from the Isle of Wight and the very top of the Dorset Wealden succession clustered together. (Samples 50AIOW, 50BIOW, 50CIOW, 50DIOW, 50EIOW, 48AIOW, 48CIOW, 48DIOW, 44AIOW, 2AD, 5D, 10D.) This is as expected considering the close stratigraphic proximity of the samples and their isolation from most of the rest of the samples that come from the lower part of the succession. A few samples that are close to this group stratigraphically did not cluster with them because of their lack of species diversity.
2. The samples from the lower to middle part of the Dorset succession clustered together in many cases. (Samples 7DD, 7BD, 8D, 18BD, 18DD, 20AD, 20BD.) The absence of samples from the south-eastern area from this group is perhaps best explained in terms of geographical differences in the flora and in the nature of the plant beds.
3. Another group of samples from the Dorset succession, but more wide-ranging than the previous group. (Samples 7AD, 11AD, 11BD, 13D, 27AD, 27BD, 27CD, 27DD, 17D, 18AD, 18BD, 18CD, 18DD, 22D.) This group encompasses the species-poor samples and those very rich in 30 CHEIR.
4. A group of species-rich samples from the Fairlight Clay of Sussex. (Samples 51BH, 41H, 13H, 18AH, 22H.) Several cuticle species are exclusive to this group.

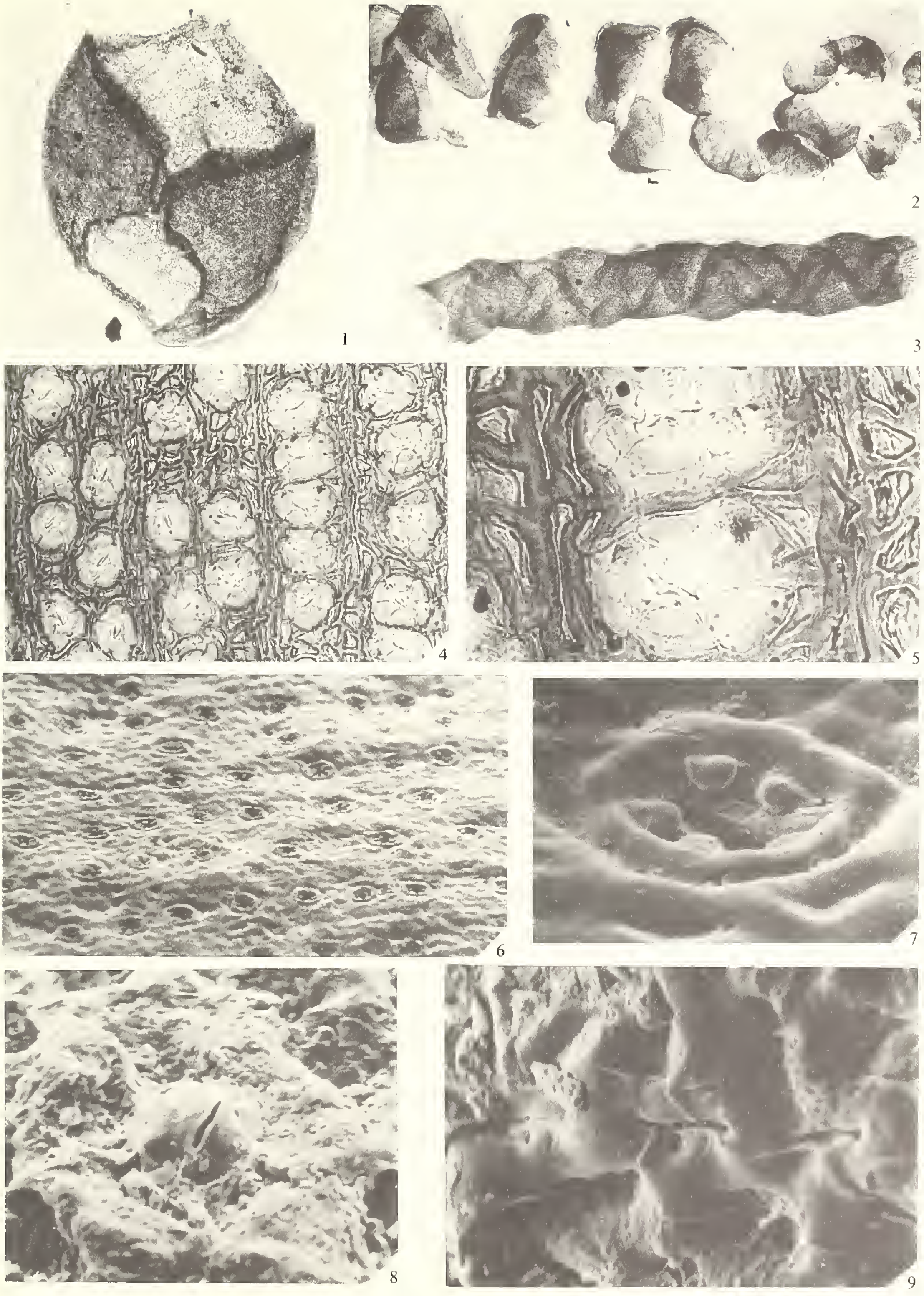
It became clear from the study that although samples that were closely related stratigraphically tended to cluster together and show high similarity coefficients this was not always the case. The coefficient of similarity between two samples only separated by a few metres of sediment can be very low indeed. There is also a tendency for species to be of similar abundance in samples closely related stratigraphically and if a species is absent from one such sample it is unlikely to be more than occasional in another.

The variation that occurred within a single band of a plant debris bed complex was determined by collecting samples at intervals along the exposed length of two bands. It was difficult to follow any band for more than four metres and more usually they petered out or merged with other bands within a metre. The two bands selected were from the south-eastern area and neither was used in the main analysis. An analysis of these two bands is presented in Table 4. Similarity coefficients were calculated for the samples from each band. Most samples showed high coefficients, but in some cases the coefficients were so low the particular samples could have been

EXPLANATION OF PLATE 72

Figs. 1, 4–9. 30 CHEIR MaA. 1, ×20, LM., leaf; P49: 3/2.1. 4, ×150, LM., abaxial surface, stomata; P49: 6/1.1. 5, ×500, LM., abaxial surface, stomata; P49: 6/1.1. 6, ×100, SEM., abaxial surface, outside, stomatal apertures; B7. 7, ×1000, SEM., abaxial surface, outside, stomatal aperture; B7. 8, ×1000, SEM., abaxial surface, inside, stoma; B12. 9, ×1000, SEM., abaxial surface, inside, hypodermis; B12.

Figs. 2, 3. Cf. 30 CHEIR MaA. 2, ×5, LM., shoot, 'exploded'; P110: 2/1. 3, ×5, LM., shoot; P130: 7/1.1.



OLDHAM, 30 CHEIR MaA and cf. CHEIR MaA

TABLE 4. Analysis of the content of two selected bands.

	BAND 1								BAND 2						
	I	H	G	F	D	C	B	A	G	F	E	D	C	B	A
2 CYCAD	–	–	–	–	–	–	–	–	3	3	3	3	3	3	3
4 CYCAD	2	–	–	–	–	–	–	–	–	–	–	–	–	1	–
6 CYCAD	2	–	–	–	–	–	–	–	–	–	–	–	–	1	1
8 CYCAD	3	2	–	2	–	2	2	–	2	2	–	–	–	2	2
10 CYCAD	–	–	–	–	–	–	–	–	2	2	2	2	3	3	3
11 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
13 BENN	–	2	2	2	2	2	2	2	–	–	–	–	–	–	2
15 BENN	2	4	3	3	3	3	3	3	–	2	1	–	3	2	3
16 BENN	2	2	3	2	2	2	2	2	2	2	2	2	3	3	3
17 BENN	–	–	2	–	–	–	2	–	2	3	2	2	3	3	3
18 BENN	3	3	3	2	3	3	3	3	–	–	–	–	–	–	–
21 BENN	2	2	–	–	2	–	2	2	–	–	–	–	–	–	2
22 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
25 GINK	2	2	3	3	2	3	3	2	2	3	2	2	3	3	3
26 GINK	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–
27 GINK	–	2	2	2	1	2	1	–	3	3	3	3	3	3	3
29 GINK	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
30 CHEIR	2	3	2	2	1	2	3	3	5	5	5	5	5	5	5
34 CONIF	2	2	3	3	2	2	2	3	2	2	2	2	2	3	3
35 CONIF	–	–	–	–	–	–	–	–	3	3	2	3	3	2	2
36 CONIF	4	4	3	3	3	3	3	3	3	3	3	4	4	4	3
38 GYMN	–	–	3	3	3	–	–	–	2	2	2	2	2	3	3
40 GYMN	–	–	2	–	–	–	–	2	–	–	–	–	2	–	2
WOOD Bl	3	3	5	5	2	2	2	2	3	4	3	3	2	2	2
WOOD Br	3	3	3	3	2	2	2	3	4	5	4	4	3	3	3
MEGASPR	2	2	2	2	2	2	2	2	2	2	2	2	–	–	1
SEEDS	–	1	2	1	2	2	2	2	2	2	2	2	2	2	2

Samples I–A from Band 1 collected at 0·3-m intervals along the length of the band. Samples G–A from Band 2 collected at 0·6-m intervals along the length of the band. See Table 1 for key to abundance scale.

suspected of being widely separated in both space and time. The range of abundance of the species present was not great within a single band. If a species was absent from one sample it was only rarely more than occasional in the other samples.

ASSOCIATION ANALYSIS

The association of each taxon with every other was calculated using the Chi square value for each pair. A probability of 1% or less was considered significant and of

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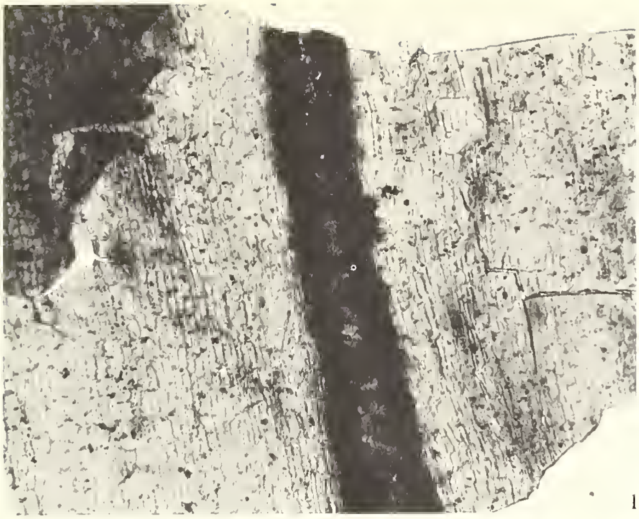
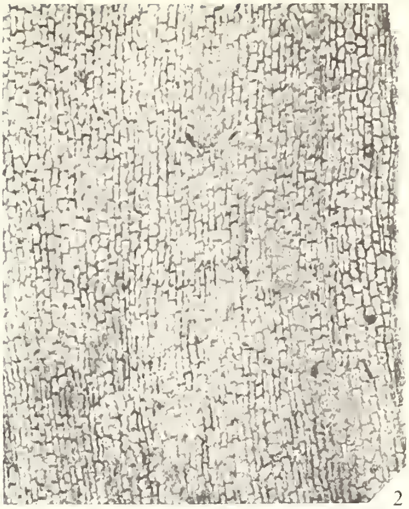
EXPLANATION OF PLATE 73

Figs. 1–6. 31 TAXOD ScA. 1, × 50, LM., surface 2, general view; P49: 40/1.1. 2, × 50, LM., surface 1, general view; P49: 40/1.1. 3, × 200, SEM., surface 2, outside, groove; B24. 4, × 1000, SEM., surface 2, outside, groove; B24. 5, × 1000, SEM., surface 2, inside, stoma; B64. 6, × 500, SEM., surface 2, inside, epidermal cells; B64.



1



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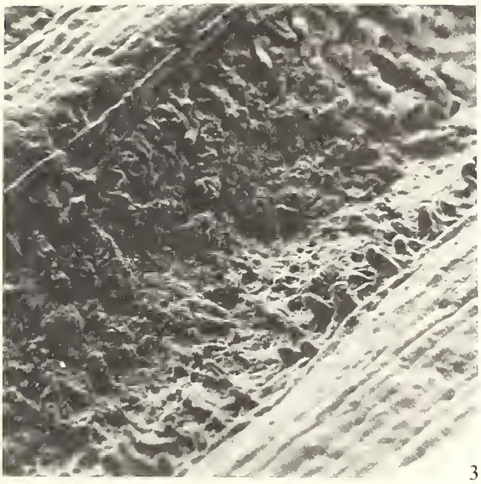

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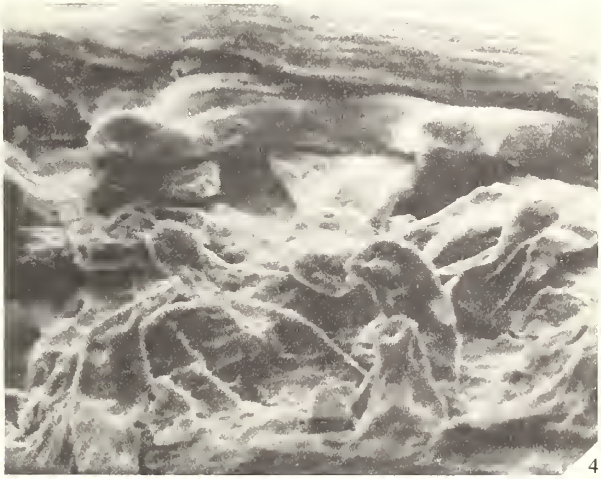

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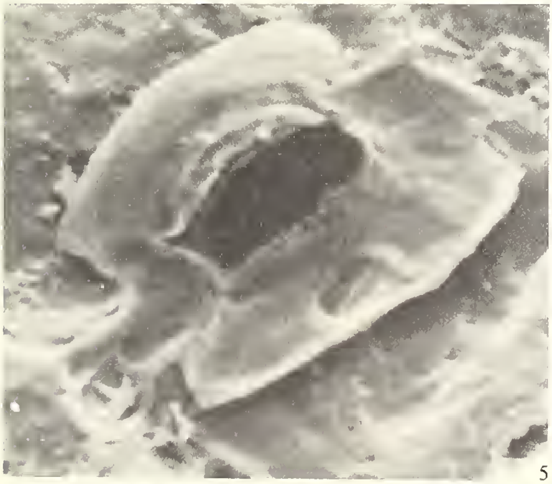

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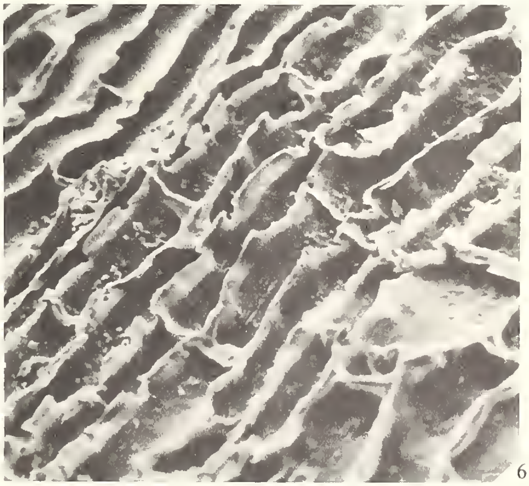

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OLDHAM, 31 TAXOD ScA

TABLE 5. Taxa showing positive associations at or below the 1% probability level.

	40 GYMN	39 GYMN	38 GYMN	37 TAXAC	35 CONIF	32 TAXOD	31 TAXOD	29 GINK	28 GINK	27 GINK	26 GINK	25 GINK	24 GINK	23 BENN	22 BENN	21 BENN	19 BENN	18 BENN	17 BENN	16 BENN	15 BENN	14 BENN	13 BENN	11 CYCAD	10 CYCAD	9 CYCAD
1 CAYT	–	3	2	–	–	–	3	–	–	2	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
2 CYCAD	–	–	3	–	–	–	–	–	–	3	–	3	–	–	–	–	–	–	–	–	–	–	2	3	3	–
4 CYCAD	–	–	–	1	–	–	2	–	–	–	–	1	–	–	–	3	2	1	2	–	–	–	2	–	–	–
5 CYCAD	2	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
6 CYCAD	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	2	–	3	–	3	3	–	–	–
7 CYCAD	–	–	3	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	3	2	2	–	3	–
8 CYCAD	–	–	–	–	–	–	–	–	–	2	2	–	–	3	–	–	3	–	3	–	–	–	2	–	–	–
9 CYCAD	2	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
10 CYCAD	–	–	3	–	–	–	3	–	–	3	–	2	3	–	–	–	–	–	–	–	3	–	3	3		
11 CYCAD	–	–	3	–	–	–	–	–	–	3	–	1	–	–	–	–	–	–	–	–	–	–	–			
12 CYCAD	2	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
13 BENN	–	2	3	–	–	–	3	–	–	3	–	3	3	–	–	–	–	3	–	3	3	2				
14 BENN	–	2	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–					
15 BENN	–	–	–	–	–	1	3	–	–	–	–	3	3	–	3	3	–	2	–	3						
16 BENN	–	–	–	–	–	–	–	–	–	–	–	1	3	–	3	–	–	2	3							
17 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–								
18 BENN	–	–	1	–	–	–	–	–	–	–	–	–	3	–	2	–	–									
19 BENN	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–										
21 BENN	–	–	2	–	1	–	3	2	–	2	–	–	–	–	1											
22 BENN	–	–	3	–	–	–	–	–	–	2	–	2	1	–												
23 BENN	–	–	–	1	–	–	–	–	–	–	–	–	–													
24 GINK	–	3	3	–	–	–	3	–	–	3	–	3														
25 GINK	–	3	3	–	–	–	3	–	–	3	–															
26 GINK	–	–	–	–	–	–	3	–	–	–																
27 GINK	–	3	3	–	–	–	–	–	–																	
29 GINK	–	–	–	–	2	–	–	–																		
30 CHEIR	–	–	–	–	2	–	–																			
31 TAXOD	2	3	–	–	–	–																				
34 CONIF	–	–	2	–	–																					

1 = 1·0% level
2 = 0·5% level
3 = 0·1% level

the 819 possible associations only 112 satisfied this requirement. These are shown in Table 5.

The following picture emerges:

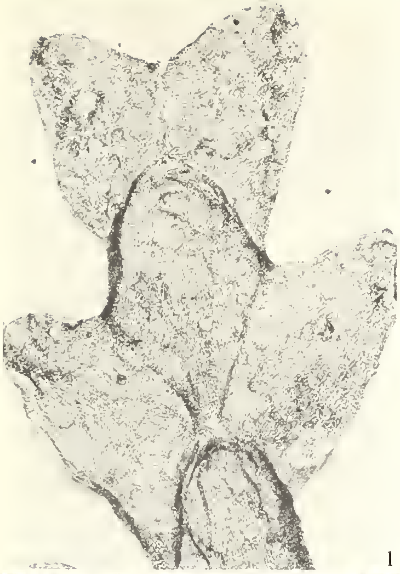
1. Those taxa that are not significantly associated with any other. This includes 3 CYCAD, 20 BENN, 33 CUPR, and 41 GYMN.

2. Those that are significantly associated with other taxa but do not form part of any mutual association group of three or more taxa. This includes 12 CYCAD, 26 GINK, 30 CHEIR, 32 TAXOD, 34 CONIF, and 37 TAXAC.

3. Those taxa that form mutual association groups of three or more taxa. There are nine of such groups, some probably representing real associations in nature, others not so.

EXPLANATION OF PLATE 74

Figs. 1–7. 33 CUPR CuA. 1, ×20, LM., shoot; P93: 3/4.2. 2, ×20, LM., shoot; P93: 3/3.2. 3, ×500, SEM., abaxial surface, inside, stoma; B21. 4, ×1250, SEM., abaxial surface, outside, stomatal aperture; B21. 5, ×20, LM., shoot; P93: 3/3.1. 6, ×150, LM., abaxial surface, stomata; P93: 5/2.1. 7, ×500, SEM., abaxial surface, inside, stoma; B21.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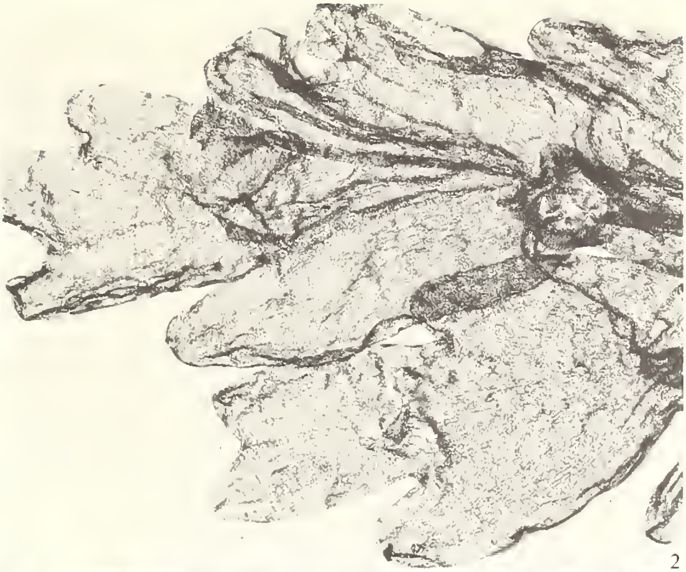
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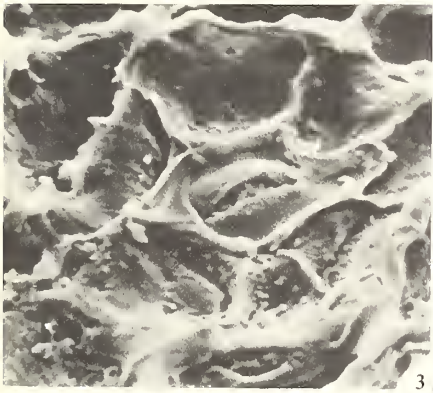
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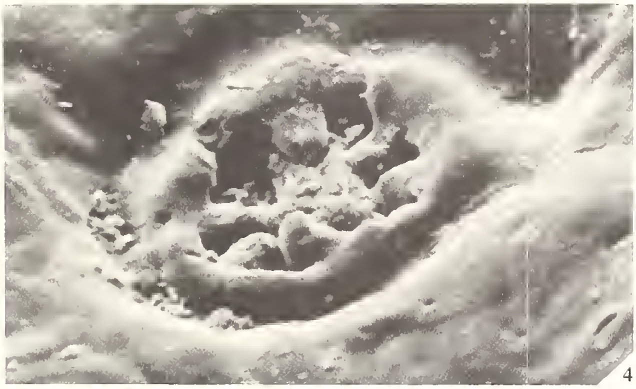
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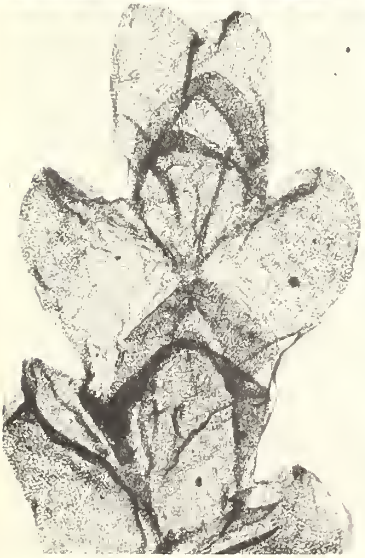
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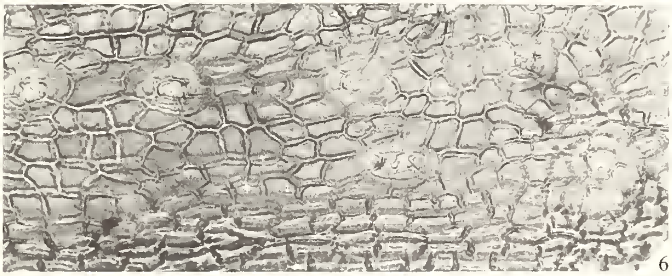
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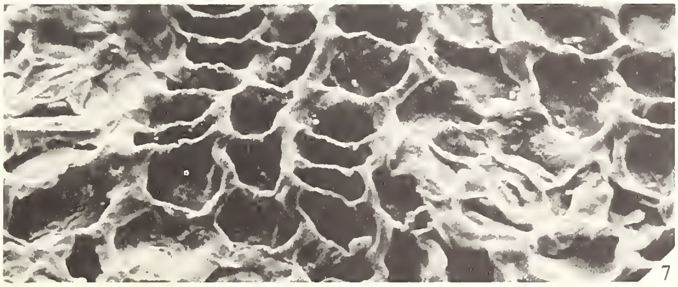
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OLDHAM, 33 CUPR CuA

Group A. 8 CYCAD, 19 BENN, and 23 BENN. These three taxa are all found in moderately species-rich samples especially from the Isle of Wight.

Group B. 1 CAYT, 27 GINK, 31 TAXOD, and 39 GYMN. Also often associated are 25 GINK and 38 GYMN. This is unlikely to be of significance as several samples rich in 1 CAYT do not fit in here.

Group C. 21 BENN, 29 GINK, and 35 GYMN. Again a group that is not likely to be of significance.

Group D. 9 CYCAD, 28 GINK, and 40 GYMN. Also often associated are 5 CYCAD and 31 TAXOD. This may well reflect the restriction of the taxa to the lower strata of the Dorset succession rather than any close association in nature.

Group E. 4 CYCAD, 21 BENN, and 31 TAXOD. This group is of doubtful significance as two of the taxa are wide-ranging.

Group F. 7 CYCAD, 13 BENN, 14 BENN, and 24 GINK. Also 39 GYMN is often associated with this group. This is a group from the species-rich beds of the Fairlight Clay.

Group G. 16 BENN, 17 BENN, and 22 BENN. A bennettitalean group.

Group H. 6 CYCAD, 13 BENN, 15 BENN, 16 BENN, 18 BENN, and 22 BENN. The largest bennettitalean group which like group G may well reflect a close association in nature.

Group I. 10 CYCAD, 13 BENN, 15 BENN, 24 GINK, 25 GINK, 27 GINK, and 38 GYMN. Also often associated are 2 CYCAD, 7 CYCAD, 11 CYCAD, 21 BENN, 22 BENN, 31 TAXOD, and 39 GYMN. This is a group of taxa from the Fairlight Clay of Sussex, many of the species being confined to this area. It may reflect a close association in nature or may simply reflect the nature of the beds involved.

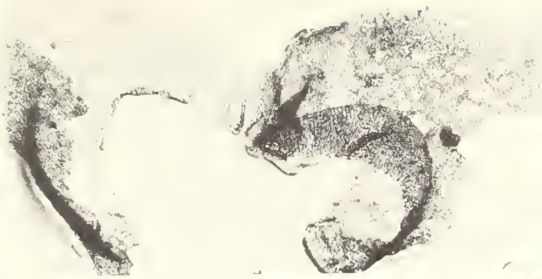
The association of other types of plant material with the samples was also examined. Seeds and brown wood showed no significant association with any factor. Black wood (*sensu* Batten 1973*a*) tended to be more abundant in the species-poor samples and especially those with poorly preserved cuticle remains. Megaspores were more abundant in those samples where the cuticle matter was of small bulk and of low species diversity. If these megaspores are from aquatic plants with correspondingly poorly cutinized parts such a result is to be expected.

LOCALITY FREQUENCY AND ABUNDANCE OF THE TAXA

The importance of the various taxa within the context of the plant debris beds can be considered in terms of presence or absence, Couper's (1958, p. 88) locality frequency, or in terms of relative abundance within each sample. These values are displayed in text-fig. 2.

EXPLANATION OF PLATE 75

Figs. 1–8. 34 CONIF BrA. 1, ×20, LM., leaf; P59: 31/1.2. 2, ×150, LM., adaxial surface; P59: 31/2.1. 3, ×20, LM., leaf; P59: 31/2.1. 4, ×1000, SEM., abaxial surface, inside, stoma; B15. 5, ×150, LM., abaxial surface, stomata; P59: 31/2.1. 6, ×200, SEM., abaxial surface, inside, stomata; B15. 7, ×500, SEM., abaxial surface, outside, general view; B65. 8, ×1000, SEM., abaxial surface, outside, stomatal apertures; B65.



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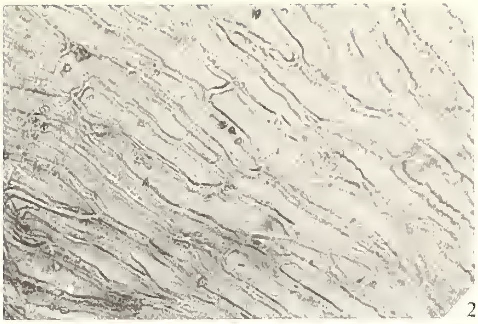

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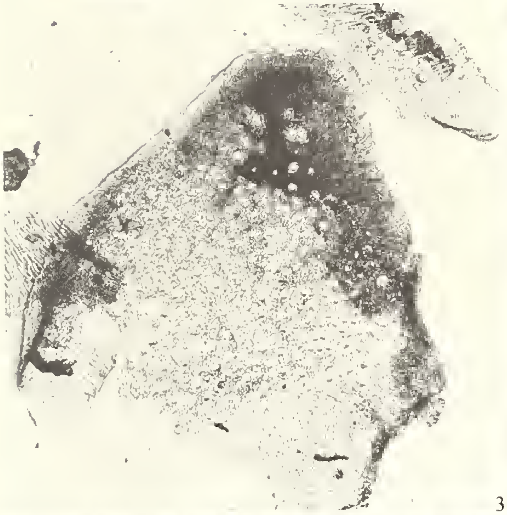

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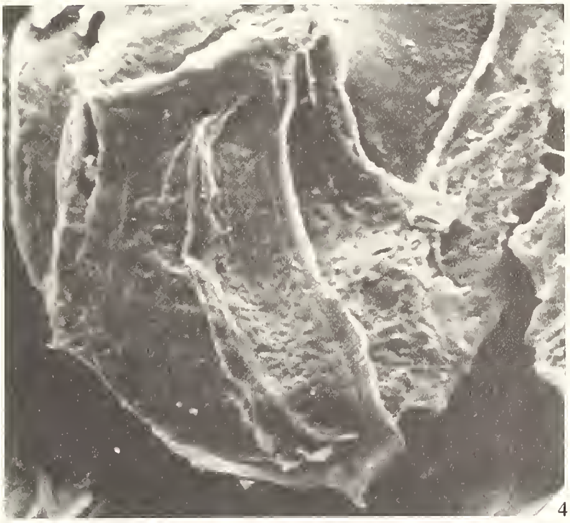

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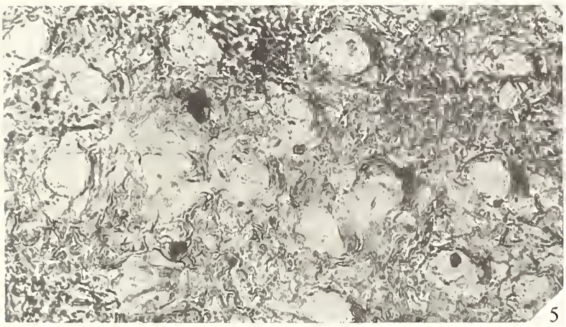

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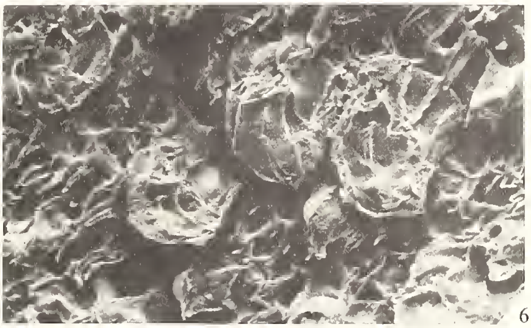

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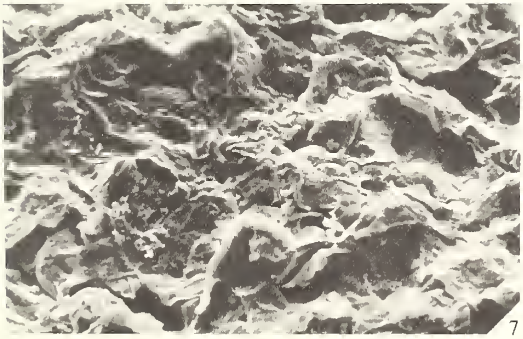

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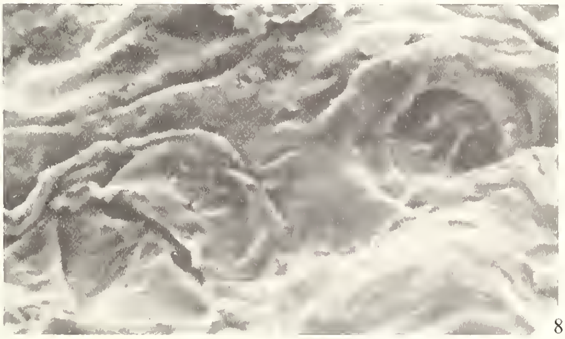

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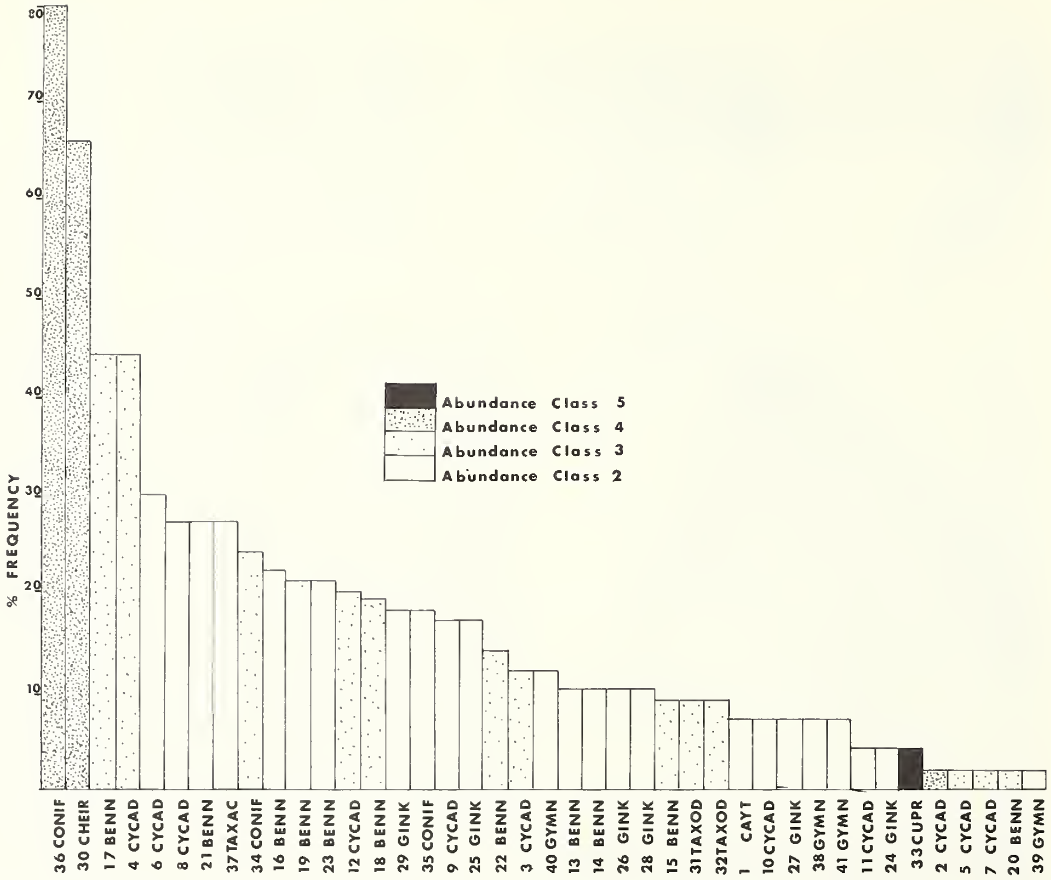
OLDHAM, 34 CONIF BrA



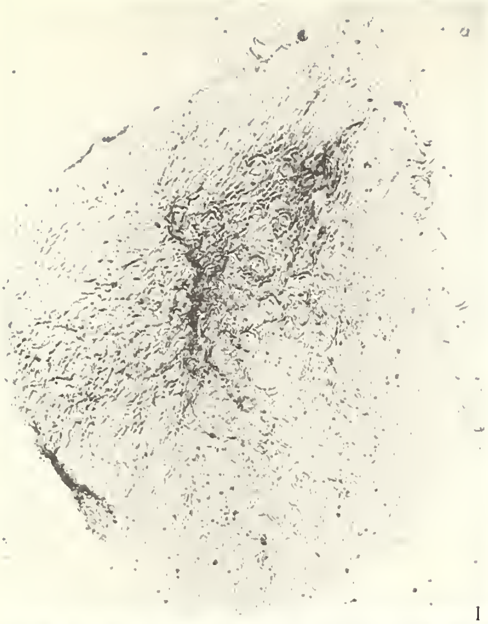
TEXT-FIG. 2. Histogram to show the locality frequency and abundance of the plant taxa.

Only 10% of the taxa have a locality frequency of greater than 30%. 30 CHEIR and 36 CONIF stand out as the two most frequent taxa, followed by 17 BENN and 4 CYCAD.

In terms of relative abundance within each sample, most taxa are only occasional. The two most frequent taxa in terms of locality frequency are also the most abundant taxa in terms of quantity of preserved material. Others, that are of low locality frequency are sometimes abundant when they do occur, for example, 33 CUPR.

EXPLANATION OF PLATE 76

Figs. 1–6. 35 CONIF BrB. 1, ×50, LM., leaf; P107: 5/3.2. 2, ×150, LM., abaxial surface, stomata; P107: 5/3.1. 3, ×500, SEM., abaxial surface, inside, stomata; B20. 4, ×500, SEM., abaxial surface, outside, stomatal apertures; B20. 5, ×2000, SEM., abaxial surface, inside, stoma; B20. 6, ×1000, SEM., abaxial surface, outside, stomatal aperture; B20.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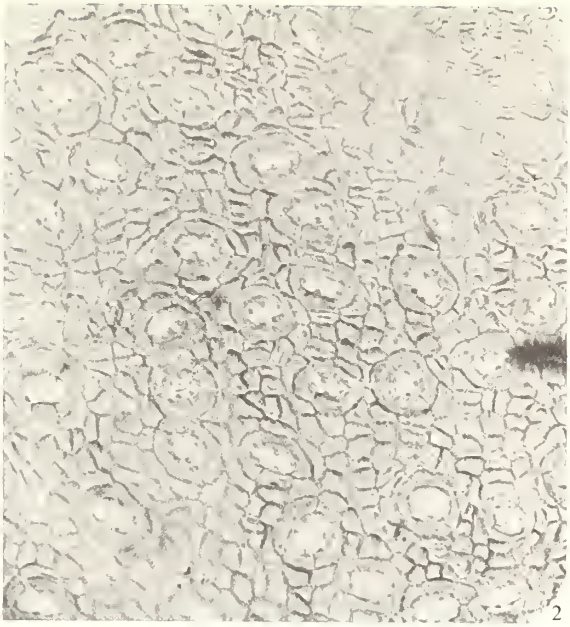
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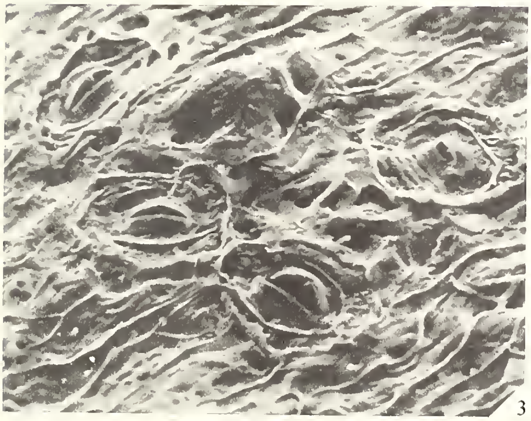
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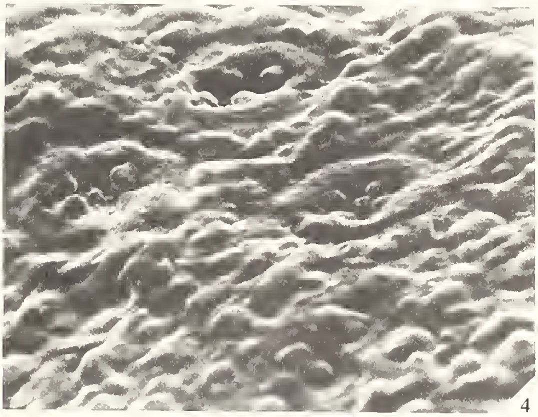
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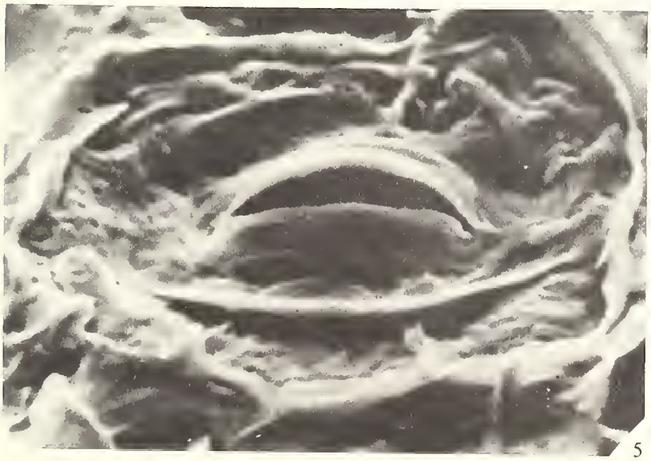
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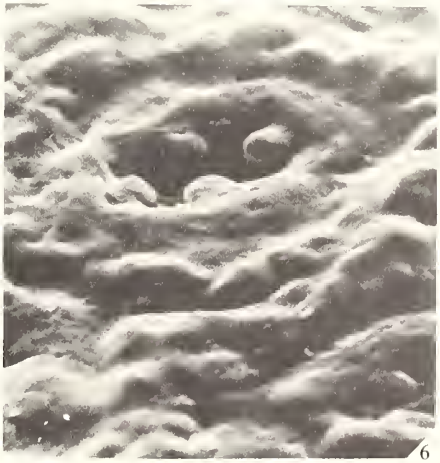
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OLDHAM, 35 conif BrB

PALYNOLOGICAL DATA

Thirty of the seventy-one samples were examined for their palynological content. The results are presented in Table 6. These data were examined to see what they revealed regarding the plant debris beds, and also to see how well they agreed with Batten's (1973*a*) assemblage types for the English Wealden, see Table 7.

Samples varied between those with only twelve genera represented to those with thirty. All of Batten's diversity classes were therefore encountered. The distribution being: small diversity 7%, average diversity 30%, and large diversity 63%. There was no marked relationship between diversity of cuticle taxa and diversity of spore genera.

Only one sample showed poorly preserved miospores but this did not show any relation to the preservation of the cuticle remains. Those with good miospore preservation also show high spore diversity and the cuticle remains of such samples are also usually well preserved. This follows Batten's (1973*a*) findings but it does not follow that if a sample contains well-preserved plant remains the miospores will be well preserved.

The picture of the brown wood, black wood, and cuticle content of the palynological preparations reflects the picture obtained from the cuticle preparations.

The distribution of *Classopollis* is of particular interest considering its probable relationship to 30 CHEIR, one of the most frequent and abundant cuticle species. *Classopollis* is present in all but two samples and frequent in nine. In all samples where 30 CHEIR is very abundant and the miospore content has been analysed *Classopollis* is frequent. The converse is true in nearly all cases.

It can be concluded that the miospore content of a sample is to some degree independent of the diversity and preservation state of the cuticular material. The factors affecting the distribution of miospores not being those necessarily affecting the distribution of cuticular material. There is, however, some relationship as is shown by *Classopollis* and 30 CHEIR.

STRATIGRAPHIC CORRELATION

The work of Hughes *et al.* (1958, 1967*a*, 1969, 1973) gives an indication of the sort of picture that could be expected when correlating the samples from the four areas studied.

The majority of the samples from the south-eastern area are from the Fairlight Clay and Ashdown Sand formations. These are considered to be Berriasian to Valanginian (Hughes 1958) and samples from them should only correlate with

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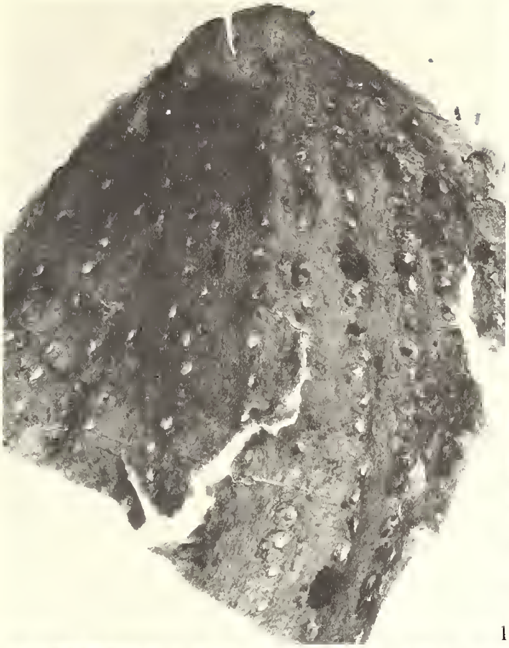
EXPLANATION OF PLATE 77

Figs. 1–7. 36 CONIF BrC. 1, ×50, LM., leaf; P98: 18/3.2. 2, ×500, LM., abaxial surface, stoma; P98: 18/2.1. 3, ×500, SEM., abaxial surface, outside, stomatal aperture; B29. 4, ×200, SEM., abaxial surface, inside, stomatal; B29. 5, ×1000, SEM., abaxial surface, inside, stoma; B29. 6, ×1000, SEM., abaxial surface, inside, hypodermis; B29. 7, ×1000, SEM., abaxial surface, outside, 'crater'; B29.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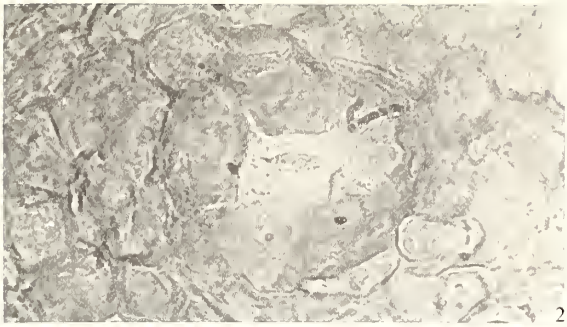
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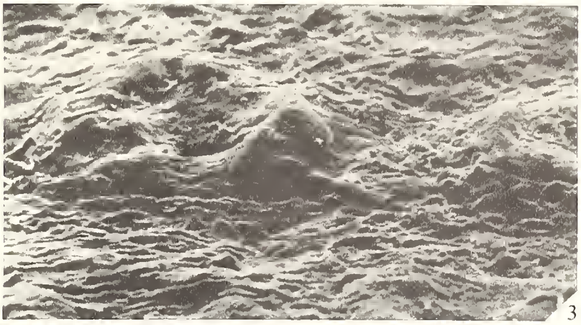
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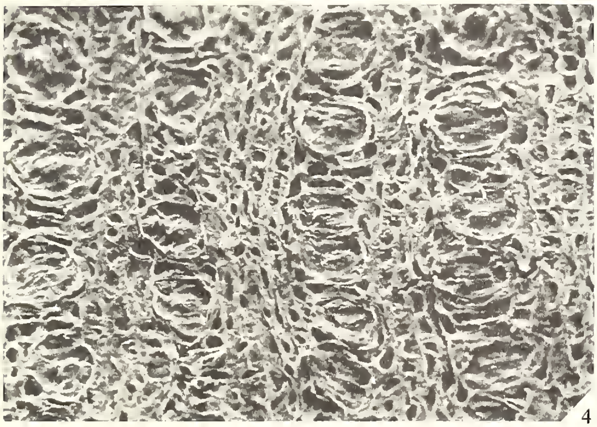
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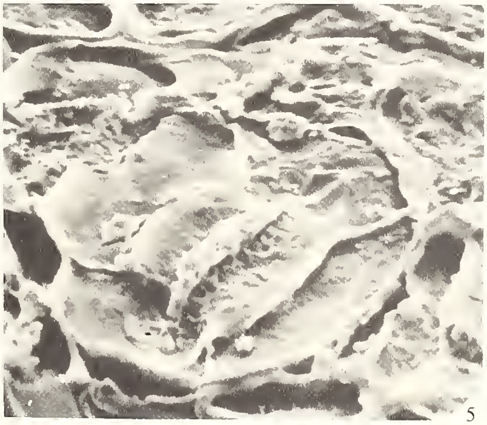
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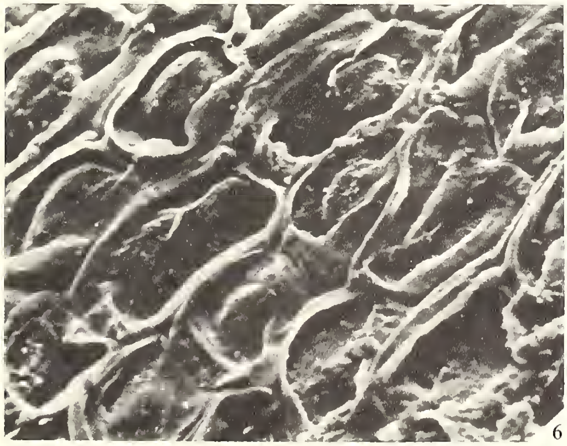
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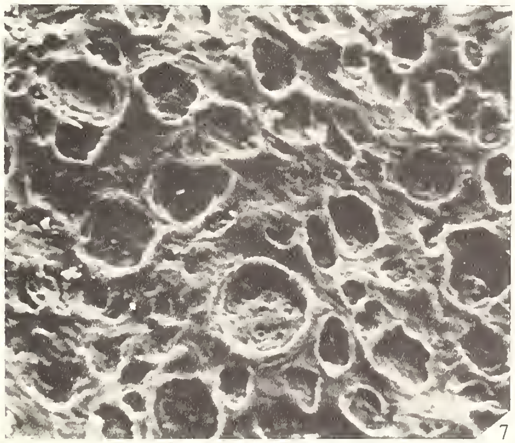
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OLDHAM, 36 CONIF BrC

TABLE 6. Miospore content of thirty selected samples.

	57H	53H	19H	22H	18AH	25H	28H	13H	41H	34AH	51BH	15AH	7AH	54H	8D	7AD	6D	5D	3AD	2AD	22D	20AD	18DD	27DD	13D	43AIOW	47IOW	48CIOW	49AIOW	50DIOW
Smooth *Triletes*	P	C	V	V	V	V	F	C	V	V	C	F	F	F	C	C	C	V	V	V	V	V	C	C	C	V	C	V	C	C
Acanthotriletes	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–
Apiculatisporis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	–
Baculatisporites	P	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	P	P	–	–	–	–	–	–
Ceratosporites	–	–	–	–	–	–	–	–	–	–	–	P	P	–	–	–	P	P	–	–	–	P	–	–	P	P	–	–	–	P
Concavissimisporites	–	–	P	P	P	P	P	P	P	P	–	P	P	C	P	P	–	–	–	–	–	–	–	P	–	–	P	P	–	P
Converrucosisporites	–	P	P	–	–	P	P	P	P	–	–	P	P	–	P	P	–	–	–	–	–	–	–	P	–	–	–	–	–	P
Kuylisporites	–	–	–	–	–	–	P	P	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leptolepidites	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	P	–	–	–	–
Neoraistrickia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	P
Osmundacidites	–	–	–	P	P	–	–	P	–	P	C	P	P	–	P	P	P	P	P	–	–	P	P	P	P	P	P	P	P	P
Pilosisporites	–	–	P	–	P	P	–	P	–	P	C	P	P	–	C	–	P	–	P	C	–	P	–	–	P	C	–	P	P	C
Verrucosisporites	–	–	–	–	–	P	P	–	P	–	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	P	–	–	–	–
Cicatricosisporites	P	P	C	C	C	C	C	C	C	C	C	C	C	C	C	C	P	P	P	V	P	C	C	C	C	P	P	C	C	V
Foveosporites group	–	–	–	–	–	–	P	–	–	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	–
Klukisporites	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lycopodiumsporites	–	–	P	P	P	–	P	P	P	P	–	C	P	–	P	–	P	P	–	–	C	P	P	P	–	–	–	P	P	P
Staplinisporites	P	P	–	–	–	P	P	P	–	P	–	–	–	–	–	–	P	–	–	P	P	–	–	P	P	–	P	–	–	P
Tripartina	–	–	–	–	–	P	–	P	–	P	P	P	–	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–
Perotrilites	–	–	P	–	–	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ischyosporites	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Matonisporites	–	P	P	–	P	P	–	–	P	P	P	P	P	P	P	–	P	P	P	P	P	P	P	–	P	P	P	–	–	P
Trilobosporites	–	P	C	P	C	C	P	P	P	P	C	P	P	P	P	–	P	P	P	–	–	P	P	P	P	–	–	P	P	–
Gleicheniidites	P	P	C	C	C	C	C	P	P	C	–	P	C	C	P	–	P	P	P	–	–	P	P	P	P	P	C	P	–	P
Contignisporites	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Densoisporites	–	P	–	–	P	–	P	P	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P
Patellasporites	–	–	–	–	–	–	–	P	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aequitriradites	P	–	–	P	–	P	P	P	P	–	–	–	P	P	P	–	–	–	P	P	–	–	–	–	P	–	–	–	–	–
Coptospora	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	P	–	–	P	–	–	–	–	–	–	–	–	–	–
Rouseisporites	–	–	P	–	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	P	P	–	–	–	P	P	–	P	–	–
Total *Triletes*	C	C	F	V	F	F	F	V	F	F	F	F	F	F	F	V	V	V	V	F	F	F	V	V	V	V	V	F	V	F
Monolites	P	–	P	P	P	P	P	C	C	P	–	C	C	P	C	–	P	P	P	P	P	P	–	P	P	P	P	P	P	C
Marattisporites	–	–	P	–	P	–	P	P	P	–	–	P	P	–	P	–	–	–	–	–	–	P	–	–	P	P	–	P	–	P
Peromonolites	–	–	P	–	–	–	–	P	P	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	P	P	C	–
Araucariacites	P	–	C	P	P	–	P	C	P	P	–	P	P	–	C	C	C	C	P	P	C	C	C	C	C	P	P	P	–	P
Inapertisporites	–	–	C	P	C	C	C	C	C	C	C	P	C	P	C	C	P	C	–	–	C	P	P	P	C	P	–	C	C	C
Inaperturopollenites	C	P	C	V	C	C	C	V	V	C	C	C	V	C	C	V	C	C	P	V	C	C	C	C	C	V	C	C	C	C

Pilasporites	F	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Reticulatasporites	P	–	P	–	–	P	P	P	P	–	–	–	P	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	–
Cerebropollenites	P	P	P	–	–	P	P	–	–	–	–	–	–	P	P	–	–	–	P	–	P	–	–	P	–	–	–	–	–	–
Tsugaepollenites	C	P	C	–	P	P	P	C	P	P	P	P	–	P	P	C	C	P	P	P	C	C	P	C	P	C	P	C	P	P
Bisaccates	C	F	V	F	F	V	V	F	V	F	C	V	V	V	V	V	C	V	C	F	C	V	V	V	V	F	F	V	C	V
Eucommiidites	–	C	P	P	P	P	P	C	P	C	–	P	P	–	P	P	P	C	P	–	–	P	–	P	–	P	P	P	–	P
Cycadopites	P	C	P	–	P	C	C	C	C	P	V	C	C	P	C	C	P	C	–	P	–	P	C	P	C	C	C	C	C	P
Clavatipollenites	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	P	V	–
Classopollis	P	F	P	C	P	–	P	C	P	C	F	P	P	P	C	C	F	C	F	P	F	V	F	F	F	–	C	C	F	P
Exesipollenites	–	–	P	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	P	–	–	–	–	–	–	P	–	–	–	–
Perinopollenites	P	–	P	C	–	–	–	P	P	P	–	–	P	–	P	–	P	C	–	–	–	C	P	P	–	–	C	C	P	–
Schizosporis	–	P	P	P	–	–	–	–	–	–	–	–	C	P	C	P	–	P	–	–	–	P	P	–	P	–	–	P	P	C
Indeter. miospores	C	C	C	C	P	P	P	P	P	P	P	C	C	P	P	P	P	P	P	P	P	C	P	P	P	P	P	P	P	C
Black Wood	V	C	C	C	C	C	C	C	C	C	C	C	C	F	C	C	C	C	C	F	P	C	C	F	P	C	F	V	V	F
Brown Wood	C	C	F	V	F	F	F	F	F	V	F	C	C	C	V	V	V	C	C	C	F	F	V	F	F	V	C	V	C	C
Megaspores	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	–	–	–	P	–	–	–	–	–	–	–	P
Cuticle	V	F	F	F	F	F	F	F	F	F	F	F	F	C	F	F	F	F	F	C	F	F	F	F	F	C	C	F	F	F
Miospore diversity	A	A	L	A	L	L	L	L	L	L	A	L	L	L	L	S	L	L	L	A	S	A	L	A	L	A	A	L	A	L
Preservation state	M	M	G	P	M	M	M	M	M	M	M	G	M	G	G	M	G	M	G	M	M	G	G	G	M	M	M	G	G	G
Density of miospores	5	5	4	1	2	2	3	2	3	3	1	4	4	5	3	1	3	3	3	2	1	3	3	4	2	2	2	2	2	4

Key to symbols in Table 6

P = less than 3% of total miospores. Present.
C = 3% to 14% of the total miospores. Common.
V = 15% to 29% of the total miospores. Very common.
F = 30% or more of the total miospores. Frequent.

Miospore diversity:

S = little diversity. 13 or fewer taxa.
A = average diversity. 14–19 taxa.
L = large diversity. 20 or more taxa.

Preservation state:

B = poor.
M = fair.
G = good.

Density of miospores:

1 = 1–19 spores per traverse.
2 = 20–49 spores per traverse.
3 = 50–99 spores per traverse.
4 = 100–199 spores per traverse.
5 = 200+ spores per traverse.

TABLE 6. Miospore content of thirty selected samples.

	57H	53H	19H	22H	18AH	25H	28H	13H	41H	34AH	51BH	15AH	7AH	54H	8D	7AD	6D	5D	3AD	2AD	22D	20AD	18DD	27DD	13D	43AIOW	47IOW	48CIOW	49AIOW	50DIOW
Smooth *Triletes*	P	C	V	V	V	V	F	C	V	V	C	F	F	F	C	C	C	V	V	V	V	V	C	C	C	V	C	V	C	C
Acanthotriletes	–	–	–	–	·	–	–	–		–	·	–	–	–	–	–	–	–	–		–	–		–	–		–	P	–	–
Apiculatisporis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–			–	–	·	–	–	–	–	P	P	–
Baculatisporites	P	–	–	–	–	–	–	–	–	–	–	–	P	–	P	–	–	–	–	·	–	–	P	P	–	–		–	·	·
Ceratosporites	·	–	–	–	–	–	–	–	–	–	–	P	P	–	–	–	P	P	–	–	–	P	–	–	P	P	–	–	·	P
Concavissimisporites			P	P	P	P	P	P	P	P	–	P	P	C	P	P	–	–	–	–	–		–	P	–	–	P	P	–	P
Converrucosisporites	–	P	P	–	–	P	P	P	P	–	–	P	P	–	P	P	–	–	–	–	–	–	–	P	–	–	–	–	–	P
Kuylisporites	–		–	–	–	–	P	P		–	P	–	·	–	–			–	–	–	–	–	–	–	–	–	–	–	–	
Leptolepidites	–	–	P	–	–	–	–	–	–	–	–	–	–	–	–		–	P	–	–	–	–	–	–	–	P	–	–	–	–
Neoraistrickia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	–		–	–	–	·	–	–	P
Osmundacidites	–	–	–	P	P	–	–	P		P	C	P	P	–	P	P	P	P	P	–	–	P	P	P	P	P	P	P	P	P
Pilosisporites	–	–	P	–	P	P	–	P	–	P	C	P	P	–	C	–	P	–	P	C	–	P			P	C		P	P	C
Verrucosisporites	–	–	–	–		P	P		P		P			–	–	–		–	P	–	–	–	–	–	–	P		–		
Cicatricosisporites	P	P	C	C	C	C	C	C	C	C	C	C	C	C	C	C	P	P	P	V	P	C	C	C	C	P	P	C	C	V
Foveosporites group	–	–	–	–	–	–	P	–	–	–	–	P	–	P	–	–	–	–	–	–	–	–	–	–	–	–	·	P	P	
Klukisporites	–	–	–	–	–	–	–	–	–	–	–		P	–	–	–	–	–	–	·	–	–	·	–	–	–	–	–	–	–
Lycopodiumsporites	–	–	P	P	P	–	P	P	P	P	–	C	P	–	P	·	P	P		–	C	P	P	P	–	–	–	P	P	P
Staplinisporites	P	P	–			P	P	P		P	–	–		–	–	–	P	–	–	P	P	–		P	P	–	P	–		P
Tripartina	·		–			P	–	P		P	P	P		P	–		–	–	P		–	–	–	–	–	–	–	–	·	
Perotrilites	–	–	P	–	–	P	–	·	–	–	–	–	–	P	–	–	–	–	–		–	–		–		–	–	–	–	–
Ischyosporites	–	–	–	–	–	–	–	–	–	–	–	–	–	P	–	·	–	–	–	–	–	–	–	–	–	–	–	–		
Matonisporites	–	P	P	–	P	P	–	–	P	P	P	P	P	P	P	–	P	P	P	P	P	P	P	–	P	P	P	–	–	P
Trilobosporites	–	P	C	P	C	C	P	P	P	P	C	P	P	P	P	·	P	P	P		–	P	P	P	P	–	–	P	P	·
Gleicheniidites	P	P	C	C	C	C	C	P	P	C	–	P	C	C	P		P	P	P	–	–	P	P	P	P	P	C	P	·	P
Contignisporites	–	–	–	–	P	–	–	–	–	–	–	–	–	–	–	·	–	–	–	–	–	–	–	–			–	–		P
Densoisporites	–	P	–	–	P	–	P	P		–	P	–	–	–			–	–	–	–	–	–	–	–	–		–	–	–	P
Patellasporites	–	·	–	–	–	–	–	P	P	–	–	–	–	P	·		–	–	–	–	–		–	–	–		–	–	–	–
Aequitriradites	P	–	–	P	–	P	P	P	P	–	–	–	P	P	P	·	–	–	P	P	–	–	–	–	P	·	–	–		–
Coptospora	·	–	–	–	–	·	–	·	–	–	–	–	–	P	–	–	P	–	–	P	–	–	–	–	–	–	–	–	–	–
Rouseisporites		–	P	–	–	–	–		P	–	–	–	–	–	–	–	–	–	–	P	P	–	–	–	P	P	–	P	–	–
Total *Triletes*	C	C	F	V	F	F	F	V	F	F	F	F	F	F	F	V	V	V	V	F	F	F	V	V	V	V	V	F	V	F
Monolites	P		P	P	P	P	P	C	C	P	–	C	C	P	C	–	P	P	P	P	P	P	–	P	P	P	P	P	P	C
Marattisporites	–	–	P	–	P	·	P	P	P	·	–	P	P	–	P			·		–	–	P	–	–	P	P	–	P	–	P
Peromonolites	–	–	P	–	–	–	–	P	P	–	–	–	–	–	–	–	–	–		–	–	P		–	–	–	P	P	C	
Araucariacites	P	–	C	P	P	–	P	C	P	P	–	P	P	–	C	C	C	C	P	P	C	C	C	C	C	P	P	P	–	P
Inapertisporites	–		C	P	C	C	C	C	C	C	C	P	C	P	C	C	P	C	–	–	C	P	P	P	C	P	–	C	C	C
Inaperturopollenites	C	P	C	V	C	C	C	V	V	C	C	C	V	C	C	V	C	C	P	V	C	C	C	C	C	V	C	C	C	C
Pilasporites	F		–	·		·	·		–	–	·			–	–	–	–	·			–			·				–		
Reticulatasporites	P	–	P	–	–	P	P	P	P	–	·	–	P	P	·	–	–	–			–	P	·	–	–		·	–		
Cerebropollenites	P	P	P	–	–	P	P		–	–	–	·	–	P	P	–	–	·	P	·	P	–		P	–	–	–	–	–	
Tsugaepollenites	C	P	C	–	P	P	P	C	P	P	P	P	–	P	P	C	C	P	P	P	C	C	P	C	P	C	P	C	P	P
Bisaccates	C	F	V	F	F	V	V	F	V	F	C	V	V	V	V	V	C	V	C	F	C	V	V	V	V	F	F	V	C	V
Eucommiidites	·	C	P	P	P	P	P	C	P	C	–	P	P	–	P	P	P	C	P	–	–	P	–	P	–	P	P	P	–	P
Cycadopites	P	C	P	–	P	C	C	C	C	P	V	C	C	P	C	C	P	C		P	–	P	C	P	C	C	C	C	C	P
Clavatipollenites			–	–		–	–	–	·	–	–	–	–	–	–	–	–	·	–	–	–	–	–	–	–	–	P	P	V	
Classopollis	P	F	P	C	P	–	P	C	P	C	F	P	P	P	C	C	F	C	F	P	F	V	F	F	F		C	C	F	P
Exesipollenites	–	–	P	–	–	–	–	P	–	–	–	–		–		–	–	–	P	–	–	–			–	P	–	–	–	
Permopollenites	P	–	P	C	–	–	–	P	P	P	–	–	P	–	P	·	P	C		–	–	C	P	P	–	–	C	C	P	·
Schizosporis	–	P	P	P	–	–	–	–	–	–	–		C	P	C	P	–	P	–	–	–	P	P	–	P		–	P	P	C
Indeter. miospores	C	C	C	C	P	P	P	P	P	P	P	C	C	P	P	P	P	P	P	P	P	C	P	P	P	P	P	P	P	C
Black Wood	V	C	C	C	C	C	C	C	C	C	C	C	C	F	C	C	C	C	C	F	P	C	C	F	P	C	F	V	V	F
Brown Wood	C	C	F	V	F	F	F	F	F	V	F	C	C	C	V	V	V	C	C	C	F	F	V	F	F	V	C	V	C	C
Megaspores			–	–		–	–		–	–	–	P	–	P	–	–	–	–	–	–	–	P	–	–	–	·	–	–	–	P
Cuticle	V	F	F	F	F	F	F	F	F	F	F	F	F	C	F	F	F	F	F	C	F	F	F	F	F	C	C	F	F	F
Miospore diversity	A	A	L	A	L	L	L	L	L	L	A	L	L	L	L	S	L	L	L	A	S	A	L	A	L	A	A	L	A	L
Preservation state	M	M	G	P	M	M	M	M	M	M	M	G	M	G	G	M	G	M	G	M	M	G	G	G	M	M	M	G	G	G
Density of miospores	5	5	4	1	2	2	3	2	3	3	1	4	4	5	3	1	3	3	3	2	1	3	3	4	2	2	2	2	2	4

Key to symbols in Table 6

P – less than 3% of total miospores. Present.
C – 3% to 14% of the total miospores. Common.
V = 15% to 29% of the total miospores. Very common.
F – 30% or more of the total miospores. Frequent.

Miospore diversity:

S – little diversity. 13 or fewer taxa.
A – average diversity 14–19 taxa.
L – large diversity. 20 or more taxa.

Preservation state:

B – poor.
M – fair.
G = good.

Density of miospores:

1 – 1–19 spores per traverse.
2 – 20–49 spores per traverse.
3 – 50–99 spores per traverse.
4 – 100–199 spores per traverse.
5 – 200+ spores per traverse.

samples from well below the 'Coarse Quartz Grit' bed in Dorset. Hughes and Croxton (1973) consider this bed to be probably late Valanginian to early Hauterivian and on this basis only samples 18AD, 18BD, 18CD, 18DD, 20AD, 20BD, and 22D from Worbarrow fall into the required category. Samples from Swanage Bay are all from above the 'Coarse Quartz Grit' except for 8D and this is only just below it. If Arkell's (1947) tracing of this bed is not altogether correct, and the botanical evidence goes some way to suggesting this, a different picture would emerge. This evidence suggests that samples 7AD, 7BD, 7DD, and 8D from Swanage Bay correlate with samples from well below the Coarse Quartz Grit bed as developed at Worbarrow Bay. If this is correct then the bed in question is not contemporaneous in the two areas.

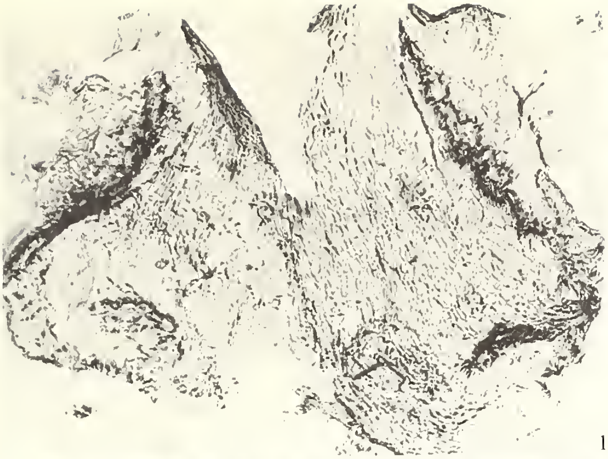
TABLE 7. Relationship of samples to Batten's (1973) assemblage-types.

	AT1	AT2	AT3	AT6	AT7	AT8	AT10	AT11	AT12	AT13	AT14	AT15	AT17
50DIOW	–	×	×	–	–	–	–	–	×	×	–	–	–
49AIOW	–	×	–	–	–	–	×	–	–	–	–	–	–
48CIOW	–	×	×	–	–	–	–	–	–	–	–	–	–
47IOW	–	–	–	–	–	–	–	–	–	–	–	–	×
43AIOW	–	–	–	–	×	–	–	–	–	×	–	–	–
13D	–	–	×		–	–	×	–	–	–	–	–	–
27DD	–	×	–	×	–	–	×	–	–	–	–	–	–
18DD	–	×	×	–	–	–	×	–	–	–	–	–	–
20AD	–	×	–	×	–	–	–	–	–	–	–	–	–
22D	–	–	–	×	–	–	×	–	–	–	–	–	–
2AD	–	–	–	–	×	–	–	–	×	×	–	–	–
3AD	–	×	×	–	–	–	×	–	–	–	–	–	–
5D	–	–	×	–	–	–	–	×	–	–	–	–	–
6D	–	×	×	–	–	–	×	–	–	–	–	–	–
7AD	–	–	–	–	×	–	–	–	–	–	–	–	–
8D	–	×	×	–	–	–	–	–	–	×	–	–	–
54H	–	×	×	–	–	–	–	–	–	–	–	×	–
7AH	–	–	×	–	×	–	–	–	–	–	–	–	–
15AH	–	×	×	–	–	–	–	–	–	–	–	–	–
51BH	–	–	–	×	–	–	×	–	–	×	×	–	–
34AH	–	–	×	–	–	–	–	×	–	–	–	–	–
41H	–	–	×	×	×	–	–	–	–	–	–	–	–
13H	–	–	×	×	×	–	–	×	–	–	–	–	–
28H	–	–	×	×	–	–	–	–	–	–	–	–	–
25H	–	–	×	×	–	–	–	–	–	–	×	–	–
18AH	–	–	×	×	–	–	–	–	–	–	×	–	–
22H	×	–	–	–	×	–	–	–	–	–	–	–	–
19H	–	×	×	×	–	–	–	–	–	–	×	–	–
53H	–	–	–	–	–	–	×	×	–	–	–	–	–
57H	–	–	–	–	–	×	–	–	–	–	–	–	–

EXPLANATION OF PLATE 78

Figs. 1–3. 32 TAXOD SpA. 1, ×50, LM., leaf; P55: 7/1.2. 2, ×150, LM., stomatal band; P55: 5/4.1. 3, ×1000, SEM., inside, stoma; B59.

Figs. 4–8. 37 TAXAC ThA. 4, ×1000, SEM., surface 2, inside, stoma; B47. 5, ×50, LM., surface 2, general view; P99: 9/2.1. 6, ×500, SEM., surface 2, outside, groove; B47. 7, ×1000, SEM., surface 2, outside, stomatal aperture; B47. 8, ×500, LM., surface 2, stoma; P99: 9/2.1.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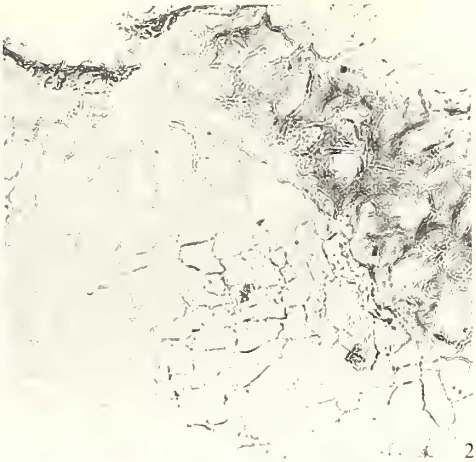
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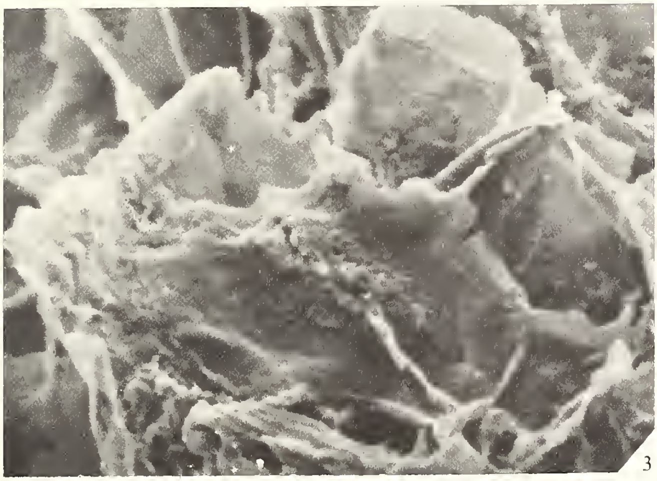
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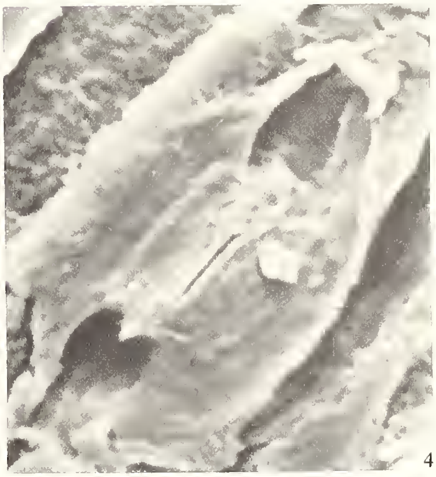
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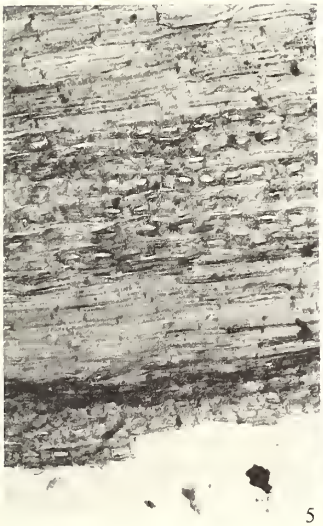
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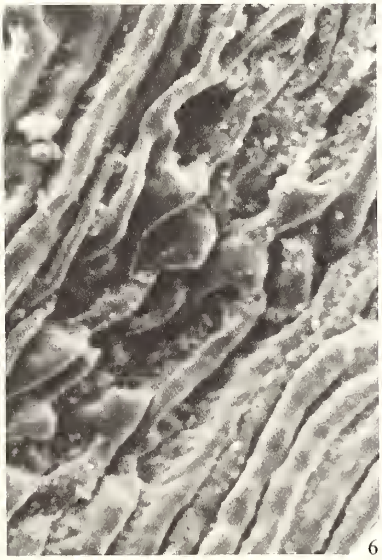
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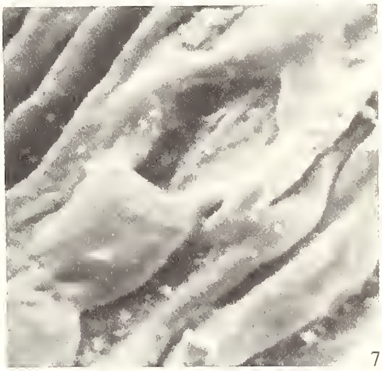
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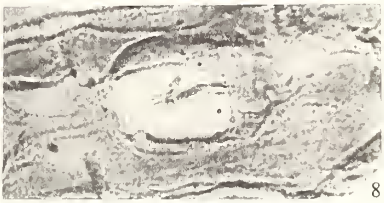
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OLDHAM, 32 TAXOD SpA and 37 TAXAC ThA

The samples from the Isle of Wight are probably Barremian to Aptian (Hughes 1958) and are well separated from all the other samples except those from the very top of the Dorset succession such as 2AD and 10D.

The majority of the samples from Swanage Bay are probably late Valanginian to early Barremian as are those from Worbarrow Bay. They should be expected to correlate well with each other but not with samples from the other areas except the few from the Tunbridge Wells Sand.

This expected picture is seen in the findings of the study. The samples from the Fairlight Clay and Ashdown Sand are well delimited by the presence of such taxa as 2 CYCAD, 7 CYCAD, 10 CYCAD, 11 CYCAD, and many bennettites including especially 13 BENN, 15 BENN, 24 GINK, 25 GINK, 27 GINK, 34 CONIF, 38 GYMN, and 39 GYMN. The absence of certain other taxa is also significant. These samples were seen to cluster out in the analysis. Their association with samples from the base of the Worbarrow succession is seen on the basis of such taxa as 28 GINK, 31 TAXOD, and 49 GYMN. That this link is not as clear as might have been hoped is probably due to the masking effect of the different sorts of debris beds in the two areas.

The samples from the Isle of Wight are delimited by the presence of 12 CYCAD, 26 GINK, and 37 TAXAC and also by the constancy of occurrence of the more wide-ranging taxa 8 CYCAD, 19 BENN, and 23 BENN. Most of the taxa of the lower strata are absent. Samples 2AD and 10D as expected fit in with this group. This grouping was also brought out in the cluster analysis.

The expected clustering of samples from Dorset was brought out in the cluster analysis. They are characterized by a high bulk of 30 CHEIR and the occurrence of 33 CUPR and 35 CONIF, both more or less confined to Dorset.

ORIGIN OF THE DEBRIS BEDS

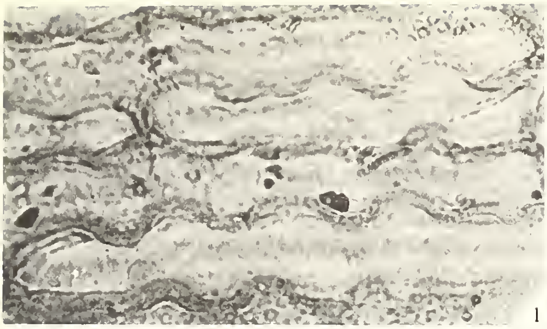
The absence of a known environmental framework within the Wessex basin and an ambiguous one in the south-eastern area make any attempt to determine the origin of the debris beds somewhat speculative. The paper by Spackman *et al.* (1969) discussing sedimentation in southern Florida is of relevance. They describe how degraded plant material is carried out into the Gulf of Mexico usually to be decomposed but occasionally to be carried by longshore currents and cast on beaches. This is normally a temporary resting place but if it becomes covered with a layer of inorganic sediment it will remain to form a lens of carbonaceous material. These deposits were examined by the author and their resemblance to those developed in the Fairlight Clay and Ashdown Sand is marked.

EXPLANATION OF PLATE 79

Fig. 1. 37 TAXAC ThA. 1, ×500, LM., surface 2, epidermal cells; P99: 9/2.1.

Figs. 2–4. 38 GYMN GyQ. 2, ×200, SEM., surface 2, outside, stomatal aperture; B52. 3, ×150, LM., surface 2, stomata; P49: 27/3. 4, ×500, LM., surface 2, stomata; P49: 27/3.

Figs. 5–8. 39 GYMN GyI. 5, ×150, LM., general view; P59: 7/4.2. 6, ×500, LM., stomatal aperture; P59: 7/4.2. 7, ×1000, SEM., inside, stoma; B43. 8, ×1000, SEM., outside, stomatal aperture; B43.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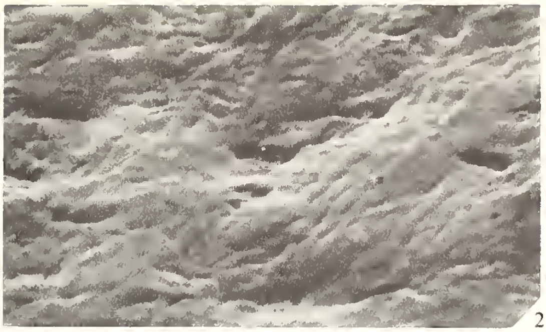
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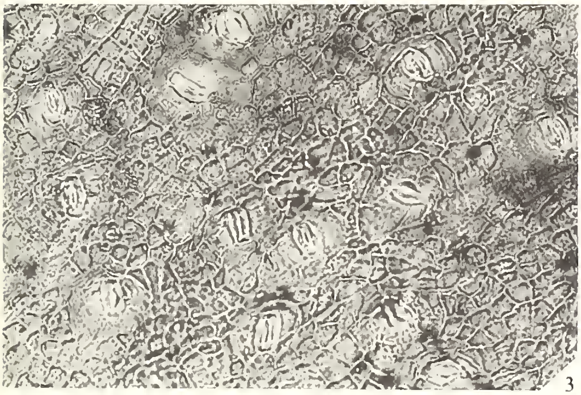
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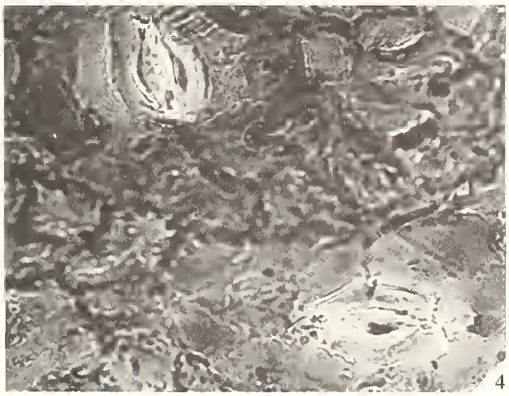
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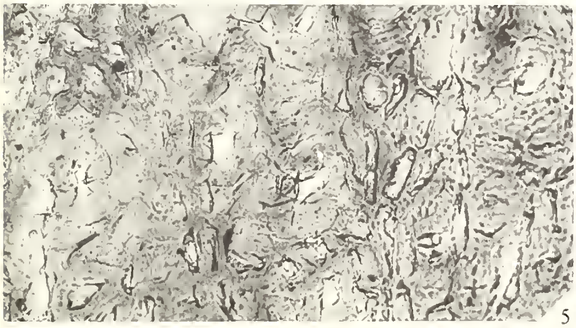
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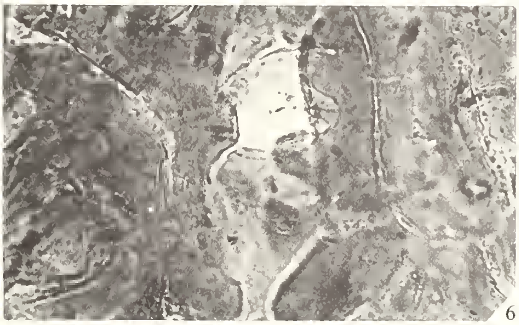
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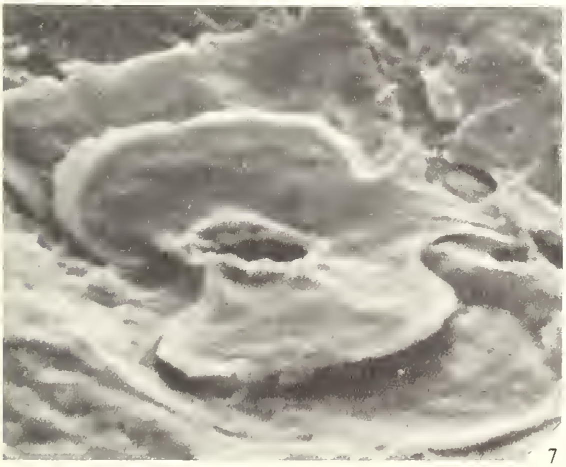
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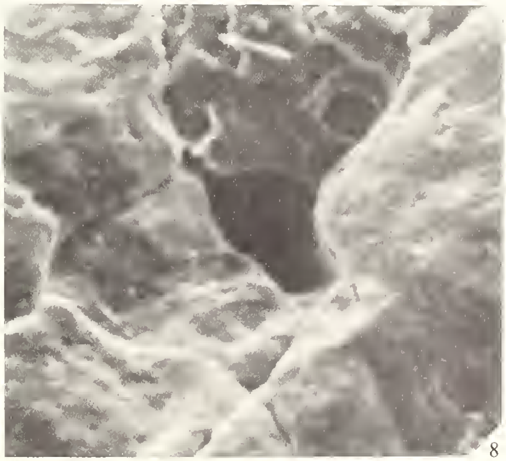
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OLDHAM, 37 TAXAC ThA, 38 GYMN GyQ, and 39 GYMN GyI

If a delta environment is invoked, as seems most probable, evidence from the debris beds suggests that they were formed on the delta top and/or shore face and delta front environments. The evidence for this is six-fold.

1. The concentration of plant material into bed complexes, each consisting of many individual beds that are short-lived and irregular in formation.
2. The thickness of some of the laminae and the composition of the material. In some cases almost pure cuticular material makes up laminae over 20 mm thick.
3. The high quality of preservation of the material, little evidence of attrition or decay, delicate structures such as hairs being intact, structure of the epidermal cell traces being clear.
4. The occurrence of beds composed almost exclusively of a single species and the implied lack of mixing of material.
5. The restriction of the beds in Sussex to the Fairlight Clay, Ashdown Sand, and Tunbridge Wells Sand. The last two of these formations are considered to have been formed in delta-front and shore-face environments by Allen (1959). He considers the Fairlight Clay to be pro-deltaic but the large numbers of megafossil and debris beds in this formation throw some doubt upon this. The absence of plant remains from the Wadhurst Clay and the Grinstead Clay, apart from equisetalean ones, which Allen also considers to be pro-deltaic also implies a different environment of origin for the Fairlight Clay.
6. The similarity of the debris beds to the plant lenses formed in the shore-face environment of southern Florida.

The plant material has obviously been transported and the main problem in accounting for the origin of the beds is the concentration of this material into thick laminae. The lagoons, active and sluggish river channels invoked by Harris (1953, 1963) to explain many of the plant beds of the Yorkshire Jurassic, are no doubt responsible in some part for the formation of the Wealden plant debris beds. The shore-face environment can be suggested as another possibility.

The source of material for the beds could be either fresh or reworked. Both sources may have been involved but the lack of megafossil beds with the Wealden suggests that much of the material must have been fresh.

The debris beds as indicators of the Wealden flora. No one type of bed in isolation can give a balanced picture of both the specific content and the relative importance of any one group within the flora. Beds rich in miospores give the most information with regard to the specific content of the flora, but as pollen from plants of bennettitalean, cycadalean, and ginkgoalean affinity tends to be under represented the

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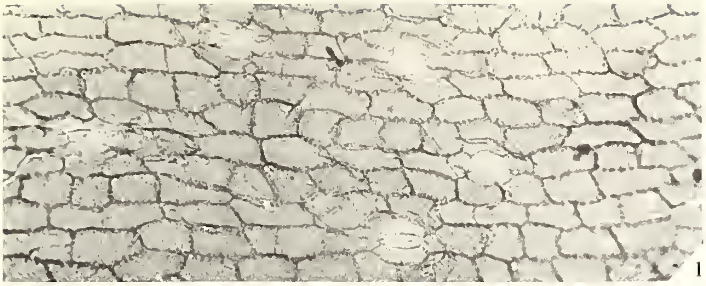
EXPLANATION OF PLATE 80

Figs. 1–4. 41 GYMN GyD. 1, ×150, LM., surface 2, general view; P98: 6/4.2. 2, ×500, LM., surface 2, stoma; P98: 6/4.2. 3, ×1000, SEM., surface 2, inside, stoma; B54. 4, ×1000, SEM., surface 2, outside, stomatal aperture; B54.

Figs. 5–8. 40 GYMN GyH. 5, ×150, LM., general view; P120: 1/3.1. 6, ×500, LM., stoma; P120: 1/3.1. 7, ×1000, SEM., inside, stoma; B56. 8, ×500, SEM., outside, stomatal apertures; B56.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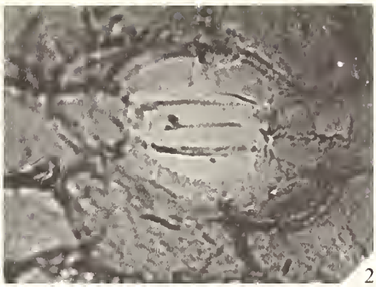
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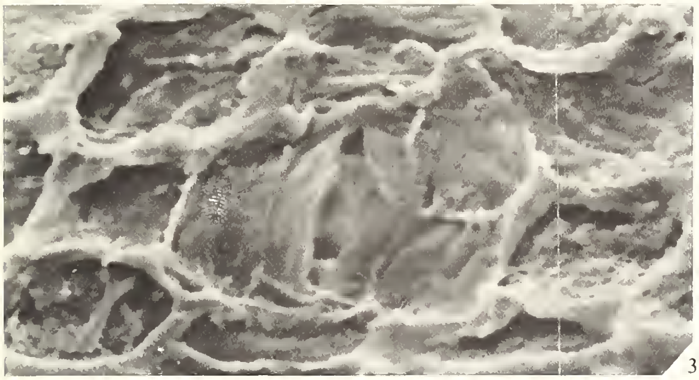
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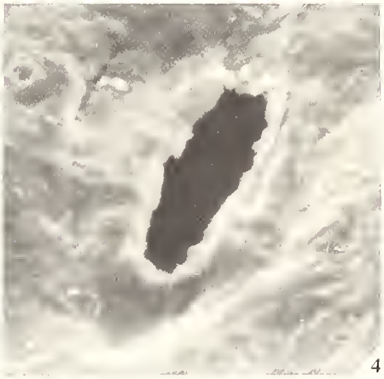
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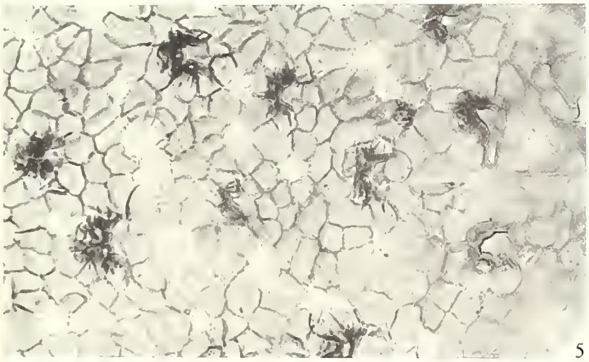
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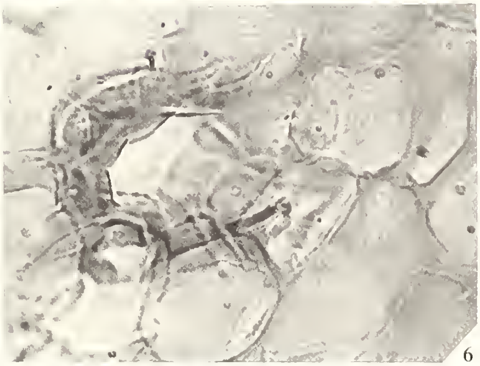
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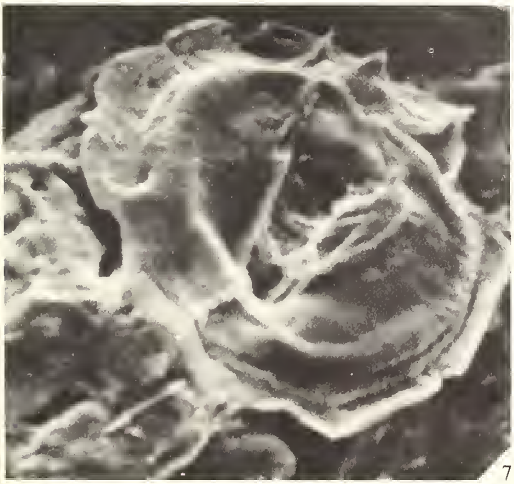
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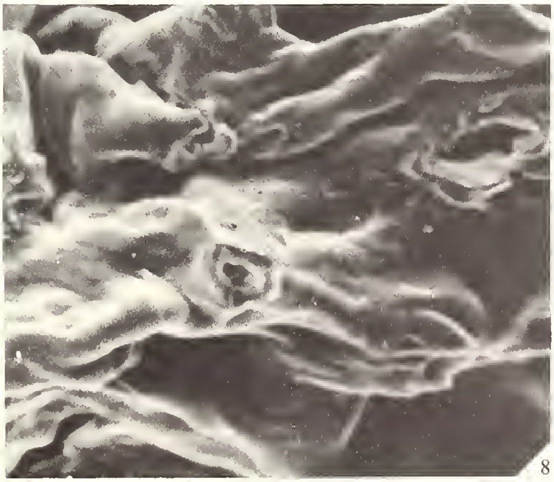
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OLDHAM, 41 GYMN GyD and 40 GYMN GhH

picture is not balanced. Megafossil beds only give an indication of a small part of the flora with waterside plants being over represented. Generalizations based upon them, especially in the Wealden where they are so scarce are suspect.

The plant debris beds fall between the two extremes. Waterside plants are again over represented and ferns are not recorded. Generalizations based upon them must be qualified, but by taking into account information from other sources a reliable picture of the flora and the relative importance of some of its members can be achieved.

THE WEALDEN GYMNOSPERMS

The Calytoniales are represented by three leaf species and the pollen grain *Vitreisporites*. Apart from the pollen grain, representatives of this group are of local occurrence only and are not found later than the Ashdown Sand in Sussex and the lower part of the Wealden Marls in Dorset. These records are some of the latest for this order.

Other plants of a possibly pteridospermous affinity have been grouped with the Cycadales in this paper. The two cuticle species relating to *Ctenozamites* are possibly pteridospermous and are found throughout the Wealden succession.

The Cycadales are not well represented in the miospore or megafossil record. The evidence from the debris beds, however, suggests that this group was of some importance, cuticle of cycadalean affinity occurring in nearly every sample studied.

The Bennettitales are second only to the Coniferae in importance and show no signs of the decline they were to undergo later in the Cretaceous. Eleven species have been described from the debris beds and several more are known only as megafossils. The large number of bennettites recorded by Daber (1960) and Benda (1961, 1962*a*, 1962*b*) from the German Wealden reinforces their importance. They tend to be associated together in samples.

The Ginkgoales are poorly represented in the miospore record but six cuticle species probably belonging to this group have been described. The group tends to favour northerly latitudes and so their presence in only a limited manner is to be expected.

The Coniferae are the major group within the flora. They are well represented in the megafossil record, are abundantly preserved as miospores, and they form by far the greatest proportion of the plant material in the debris beds. A few species may well have dominated large areas as the total number of species is low compared to the bulk of material.

The Cheirolepidiaceae as represented by 30 CHEIR and some of the *Brachyphyllum* species could be regarded as the most important Wealden family.

The Araucariaceae is only known from the Wealden as miospores and other reproductive structures. The lack of material suggests only a minor role for this family or a source at some distance from the major distributaries.

The Cupressaceae only became important in the Tertiary. Their occurrence in the Wealden is spasmodic but they are of some abundance when they do occur. This suggests a specialized habitat requirement.

The Taxodiaceae are prominent in the mid Tertiary and were only beginning their development in the Cretaceous. The appearance of a few species of local occurrence is to be expected and is found.

The Pinaceae, like the Cupressaceae, are not an important Mesozoic group and are only known from pollen grains and other reproductive structures.

The gross form of all these conifers is unknown but present-day species suggest they were likely to have been trees. The large bulk of wood present in the sediments goes some way to support this view. Wooded scenery may well have been developed over much of the delta top. Hughes and Moody-Stuart (1967*a*) invoke a mangrove type of vegetation to explain the distribution of *Classopollis* in Wealden sediments. This is of special interest considering the association of this pollen grain with 30 CHEIR.

The only representative of the Taxales is one cuticle species. In view of Florin's (1958) paper showing the importance of this group within the Mesozoic their virtual absence in the Wealden is surprising.

POSSIBLE FORM OF THE WEALDEN VEGETATION

In attempting to visualize the form and composition of the plant communities that were developed in the Wealden the botanist is faced with several problems. The sort of environment that was found in the Wealden would nowadays be dominated by angiospermous plants, many of them of a herbaceous nature. The gymnosperms that must have filled these niches in Mesozoic times are now extinct and their living relatives confined, for the most part, to high altitudes and high latitudes.

In southern Florida a combination of features occur that bear a resemblance to certain features that were probably developed in the English Wealden. This area was visited to see what light it could throw upon the problem of Wealden vegetation.

It is a low-lying area, generally wet, and supporting several gymnosperm-dominated communities. Extensive areas of arborescent angiosperms in semi-aquatic conditions also occur.

The most obviously comparable community is the cypress swamp. Pure stands of the gymnosperm *Taxodium distichum* and the exclusion of angiosperms except for a few epiphytes and creepers and the luxuriant growth of ferns, comprise a community that could well have been present in the Wealden. The ability of *T. distichum* to flourish whilst being constantly innundated by water points to a way of life that could have been of value in the wet, low-lying Wealden delta.

The succession within the cypress swamp and the gradual build up of plant material that allows other species to come in gives an example of how several different niches can be brought about solely through the agency of the vegetation from a previously flat plain. Indeed, the tree hammocks that rise above the sawgrass marsh, and are such a feature of Florida, suggest an explanation of where many of the non-water tolerant gymnosperms could have lived. Previous ideas place such plants at a distance from the delta on high ground. The considerable quantity of well-preserved plant remains at a considerable distance from any high ground could not be explained by such ideas, but by invoking tree hammocks the problem is solved.

The large variation in vegetation brought about by the slightest changes in elevation suggests that a variety of communities could have been developed on the Wealden delta. Of interest here are the pine flatwood developed on well-drained sandy soil, only 5 m above sea level. The gymnosperm *Pinus elliotti* forms an open stand with the saw palmetto *Serenoa repens* forming the main ground cover. This plant could be likened to the habit of the Mesozoic cycads and bennettites. The living cycad *Zamia integrifolia* also forms part of the ground cover in this community.

The possibility previously mentioned concerning the mangrove habit of 30 CHEIR is strengthened by an observation of the mangrove swamps of Florida. The trees line the distributaries and form a belt along the shore. Species diversity is extremely low, the vegetation being very monotonous. 30 CHEIR could well fit into this niche and its occurrence as almost the only species in several samples could be so explained.

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APPENDIX

LOCATION OF SAMPLES MENTIONED IN THE TEXT

1. *Samples from the cliff sections in the Hastings area*

Ashdown Sand

7AH	Medium grey, fine siltstone, plant material concentrated in laminae; 0·3 m above beach, Haddock's Rough, TQ 881122.
14H	Medium light grey, coarse siltstone, plant material dispersed in irregular laminae; 3 m above beach, Cliff End, TQ 885125.
15AH	Medium light grey, coarse siltstone, plant material dispersed irregularly through the matrix; Haddock's Rough, TQ 882123.
47H	Light grey, fine siltstone; plant material dispersed irregularly through the matrix; 3 m above beach, Little Galley Hill, TQ 767069.

Fairlight Clay

13H	Medium light grey, fine siltstone, plant material concentrated in laminae; 3 m above beach, Ecclesbourne Glen, TQ 837099.
18AH	Medium dark-grey siltstone, plant material concentrated in laminae; 2·5 m above beach, Haddock's Rough, TQ 878116.
19H	Medium light grey, fine siltstone, plant material dispersed irregularly through the matrix; 1 m above beach, Haddock's Rough, TQ 877116.
21BH	Light-grey siltstone, plant material concentrated in laminae; 4·5 m above beach, Lee Ness, TQ 870112.
22H	Light medium grey, fine siltstone, plant material dispersed in fine laminae; 15 m above beach, Lee Ness, TQ 868112.
23H	Light-grey siltstone, plant material concentrated in laminae; 15 m above beach, Lee Ness, TQ 866111.
25H	Medium light-grey siltstone, plant material dispersed irregularly through matrix; 6 m above beach, Warren Glen, TQ 863109.
26H	Light grey, fine siltstone, plant material dispersed irregularly through the matrix; 6 m above beach, Warren Glen, TQ 861108.
27H	Light medium-grey siltstone, plant material dispersed irregularly through matrix; 1 m above beach, Warren Glen, TQ 857108.
28H	Light grey, fine siltstone, plant material dispersed irregularly through the matrix; 4·5 m above beach, as 27H.
30H	Light-grey siltstone, plant material dispersed irregularly through the matrix; 1 m above beach, Warren Glen, TQ 856107.
32H	Light grey, fine siltstone, plant material in laminae; 0·3 m above beach, Warren Glen, TQ 855107.
33H	Light medium-grey siltstone, plant material dispersed irregularly through the matrix; 9 m above beach, Fairlight Glen, TQ 853106.
34AH	Light medium-grey siltstone, plant material in laminae; 4·5 m above beach, East Cliff, TQ 835097.
41H	Light-grey siltstone, plant material dispersed in irregular laminae; 2·5 m above beach, Ecclesbourne Glen, TQ 837099.
44H	Medium-grey siltstone, plant material concentrated in thick laminae; 5·5 m above beach, Ecclesbourne Glen, TQ 842107.
51BH	Medium grey, fine siltstone, plant material concentrated in very thick laminae; 5·5 m above beach, Galley Hill, TQ 761077.

2. *Samples from the South-east of England apart from the Hastings area*

Wadhurst Clay

54H	Medium light-grey siltstone, plant material dispersed irregularly through the matrix; 11 m below top of the Wadhurst Clay, High Brooms Brickyard, Southborough, TQ 593418.

Purbeck

53H	Medium-grey claystone, plant material in irregular laminae; River Line, Netherfield, TQ 715192.
57H	Medium-grey siltstone, plant material dispersed irregularly through the matrix; Darwell Stream, Crackle Street, TQ 696200.

3. *Samples from the Cuckfield No. 1 Borehole, Sussex* (TQ 29612731)

(Sample numbers indicate depth to the nearest foot)

CUC431	Light-grey siltstone, plant material concentrated in thin laminae.
CUC434	Light-grey siltstone, plant material concentrated in thin laminae.
CUC443	Medium light-grey siltstone, plant material in laminae.
CUC634	Medium-grey siltstone, plant material concentrated in laminae.
CUC635	Light-grey siltstone, plant material concentrated in laminae.
CUC931	Medium light-grey siltstone, plant material in laminae.

4. *Samples from Swanage Bay*

Wealden Marls

2AD	Light-grey siltstone, plant material dispersed in irregular laminae; 18 m above beach, SZ 037807.
3AD	Light grey, coarse siltstone, plant material concentrated in laminae; 6 m above beach, SZ 036806.
3BD	Light grey, coarse siltstone, plant material in irregular laminae; 0·1 m below 3AD.
5D	Light-grey siltstone, plant material concentrated in laminae; 9 m above beach, SZ 035805.
6D	Light-grey siltstone, plant material irregularly dispersed through the matrix; 6 m above beach, SZ 035805.
7AD	Medium light-grey siltstone, plant material concentrated in laminae; 5 m above beach, SZ 033799.
7BD	Medium light-grey siltstone, plant material dispersed irregularly through the matrix; 0·3 m above 7AD.
7DD	Medium light-grey siltstone, plant material dispersed irregularly through matrix; 3 m above 7AD
8D	Medium light-grey siltstone, plant material concentrated in laminae; 9m above beach, SZ 033798.

5. *Samples from Worbarrow Bay*

Wealden Marls

10D	Medium light-grey claystone, plant material dispersed irregularly through the matrix; Bed 26, SY 865803.
11AD	Light grey, coarse siltstone, plant material concentrated in laminae; Bed 23, SY 866803.
11BD	Medium light-grey siltstone, plant material in irregular laminae; 0·5 m below 11AD.
13D	Medium light-grey siltstone, plant material dispersed irregularly through the matrix; Bed 16, SY 867802.
17D	Light-grey claystone, plant material irregularly dispersed through the matrix; Bed 3, SY 869799.
18AD	Medium light-grey claystone, plant material irregularly dispersed through the matrix; Bed 3, SY 869799.
18BD	Light-grey claystone, plant material irregularly dispersed through the matrix; 0·6 m below 18AD.
18CD	Light-grey siltstone, plant material concentrated in laminae; 3 m below 18AD.
18DD	Medium light-grey claystone, plant material irregularly dispersed through the matrix; 4 m below 18AD.
20AD	Light grey, fine siltstone, plant material in irregular laminae; 5 m below 18AD.
20BD	Light grey, fine siltstone, plant material in irregular laminae; 5·5 m below 18AD.
22D	Light-grey siltstone, plant material concentrated in laminae; Bed 2, SY 870798.
27AD	Light-grey siltstone, plant material in irregular laminae; Bed 12, SY 868801.
27BD	Light grey, fine siltstone, plant material concentrated in irregular laminae; 0·2 m below 27AD.
27CD	Light-grey siltstone, plant material in irregular laminae; 0·3 m below 27AD.
27DD	Light-grey claystone, plant material in irregular laminae; 0·5 m below 27AD.

(The Bed numbers are those used in Arkell 1947.)

6. *Samples from the Isle of Wight* (all from the south-west coast)

Wealden Shales

47IOW	Medium light-grey claystone, plant material irregularly dispersed through the matrix; 3 m above beach, Shepherd's Chine, SZ 446798.

Wealden Marls

39IOW	Medium-grey siltstone, plant material dispersed irregularly through the matrix; 14 m above beach, Chilton Chine, SZ 404824.
40IOW	Medium-grey claystone, plant material dispersed irregularly through the matrix; 0·6 m below 39IOW.
41IOW	Medium-grey claystone, plant material in irregular laminae; 5 m above beach, Chilton Chine, SZ 409822.
42BIOW	Light-grey siltstone, plant material in fine laminae; 10 m above beach, Chilton Chine, SZ 409822.
43IOW	Medium-grey siltstone, plant material in irregular laminae; 6 m above beach, Grange Chine, SZ 418818.
44IOW	Medium light-grey siltstone, plant material dispersed irregularly through the matrix; 14 m above beach, Grange Chine, SZ 421817.
48AIOW	Medium light-grey siltstone, plant material concentrated in thick laminae; 6 m above beach, Brook Chine, SZ 383837.
48CIOW	Medium light grey, fine siltstone, plant material in fine laminae; 0·5 m below 48AIOW.
48DIOW	Medium grey, fine siltstone, plant material in irregular laminae; 0·7 m below 48AIOW.
49AIOW	Light-grey siltstone, plant material in irregular laminae; 1 m above beach, Compton Grange Chine, SZ 378837.
49BIOW	Light-grey siltstone, plant material in irregular laminae; 1 m above 49AIOW.
50AIOW	Medium light-grey siltstone, plant material in fine laminae; 3 m above beach, Compton Grange Chine, SZ 373847.
50BIOW	Medium light-grey siltstone, plant material in fine laminae; 0·2 m below 50AIOW.
50CIOW	Medium light-grey siltstone, plant material in fine laminae; 0·7 m below 50AIOW.
50DIOW	Medium-grey siltstone, plant material in irregular laminae; 1·7 m below 50AIOW.
50EIOW	Medium light-grey siltstone, plant material in irregular laminae; 3 m below 50AIOW.

AN EVALUATION OF AN INDEX OF AFFINITY FOR COMPARING ASSEMBLAGES, IN PARTICULAR OF FORAMINIFERA

by M. J. ROGERS

ABSTRACT. An index of affinity which is related to the city block metric is described. Its values are found to be comparable with values derived from Pearson's coefficient of contingency when model sample assemblages are used. The value of the index of affinity which indicates that samples are taken from the same assemblage varies with the type of assemblage being sampled. This critical value can be calculated by using a simple formula. Analyses of samples of recent foraminiferal assemblages from the coast of California and the Western Approaches to the English Channel agree, in general, with results obtained using traditional techniques and factor analysis. The index of affinity is very simple to calculate and is equally effective if one or many pairs of samples are being compared.

A NATURAL assemblage is not always a homogeneous unit and the species are not always randomly distributed. As Buzas (1965) found, the chi-square test showed that two samples, taken from the same place at the same time, apparently were samples from different assemblages. This is due to the test's sensitivity to lack of homogeneity between samples. A simple similarity measure, here called the index of affinity, has been used by Sanders (1960) in work on the soft-bottom community and Murray (1973) in work on Foraminifera, but the meaning of its values has been only intuitively understood as yet. The index of affinity is derived from the Manhattan or city block metric which has been used in palynology by Gordon and Birks (1972, 1974) and Birks (1974), and is closely related to the mean character difference used by Cain and Harrison (1958) and Czekanowski (1909). It is the purpose of the present paper to show how the index of affinity varies under certain circumstances and to see whether analyses based on it are approximately as effective as those based on more rigorous analyses such as chi-square and factor analysis.

The variation of the index of affinity was investigated using artificial assemblages. Samples were taken from these assemblages using a random-number generator. The index of affinity and a coefficient based on chi-square were calculated for each sample pair from a particular assemblage. The frequency distribution for the two measures of similarity was then found for each artificial assemblage. The results obtained using the artificial assemblages were then applied to a series of samples taken from two very different natural assemblages. A comparison was made between factor analysis (Streeter 1972) and an analysis based on the index of affinity using Phleger's (1964) Gulf of California samples.

Once a measure of similarity was accepted, there still remained the problem of grouping sample assemblages. This is a trivial problem when few samples are involved. For large numbers of samples cluster analysis may be used, and there are various methods of grouping or splitting collections of samples. For useful summaries see Sokal and Sneath (1963), Sneath and Sokal (1973), and Cormack (1971). In this paper a pair-group method was used to see whether the sample assemblages

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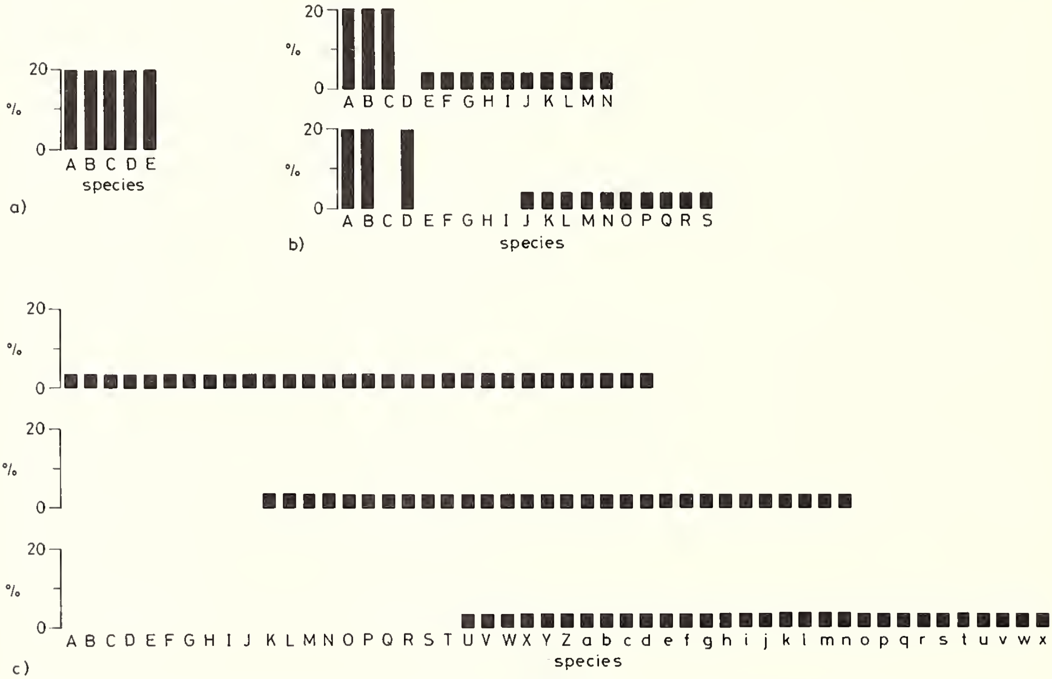
group readily. Inter-group and within-group frequency distributions were then drawn for the major groups. Using these methods it is possible to make certain statements about the assemblage (or assemblages) from which the samples were drawn and suggest areas where closer inspection of the data should be concentrated.

METHOD

To test the distribution of the index of affinity and the coefficient of contingency 100 samples were taken from an artificial assemblage and each sample contained 250 random numbers. Five artificial assemblages were designed. The first assemblage contained five equally abundant species (text-fig. 1*a*). The range of random numbers was divided into five equal parts and as each of the 250 random numbers in a sample was generated it was assigned to the part (or species) which contained that number. In three other artificial assemblages, 10, 20, and 30 species were equally represented. The fifth artificial assemblage had three species of 20% abundance each and ten species of 4% abundance. These artificial assemblages could represent biocoenoses or thanatocoenoses from which random samples were drawn. The five-species assemblage might represent a restricted environment such as a marsh or desert.



TEXT-FIG. 1. Bar diagrams showing the distribution of species in three models. *a*, one artificial assemblage containing five equally abundant species. *b*, two artificial assemblages are shown, each containing three species at 20% abundance and ten species at 4% abundance. Two species at 20% abundance and five species at 4% abundance are common to both assemblages. *c*, three artificial assemblages shown out of a possible twenty. Each assemblage contains thirty equally abundant and adjacent species selected from a line of fifty available species.

The thirty-species assemblage could represent a more equable environment such as a shelf sea or temperate grassland. In fact, most natural environments have a few dominant species with varying numbers of less-abundant species and the last artificial assemblage may most nearly resemble a biocoenose.

Having used samples from the same artificial assemblage to establish how the value of the index of affinity and the coefficient of contingency varied with the composition of the assemblage, samples from different artificial assemblages were compared. For example, fifty samples were taken from an assemblage of five species and fifty samples were taken from an assemblage of ten species (five species being common to both assemblages). In the last pair of artificial assemblages two of the species of 20% abundance were common to all samples, as were five of the species of 4% abundance, but the third species of 20% abundance and five species at 4% abundance differed in the two blocks of fifty samples (text-fig. 1*b*). A final model was designed to represent a gradual change in the biocoenose from, for example, a mud community to a sand community. A total of fifty species (*A*–*x*) were present, but each artificial assemblage contained only thirty equally abundant and adjacent species. Text-fig. 1*c* shows three of the artificial assemblages. The two upper assemblages have twenty species in common as do the two lower assemblages, but the upper and lower (which are the most dissimilar) have only ten species in common.

The city block metric is defined as follows

$$\mathrm{C.B.}_{kj} = \sum_{i=1}^{n} \left| X_{ki} - X_{ji} \right|$$

where $i = i$th species; $k, j =$ samples; $n =$ total number of species.

The index of affinity is calculated only on percentage data and, using the same notation, may be defined

$$\mathrm{I.A.}_{kj} = \sum_{i=1}^{n} \min\,(X_{ki}, X_{ji}).$$

If the data are in percentage then C.B. varies from 0 to 200, and the index of affinity, which varies from 0 to 100, equals $(100 - \frac{1}{2}\mathrm{C.B.})$.

The value of chi-square for two samples, j and k, is given by the following equation

$$\chi^2 = \sum_{i=1}^{n} \frac{(X_{ji} - EX_{ji})^2}{EX_{ji}} + \sum_{i=1}^{n} \frac{(X_{ki} - EX_{ki})^2}{EX_{ki}}$$

where degrees of freedom $= n - 1$; $X_{ji} =$ number of observations of ith species in sample j; $EX_{ji} =$ expected value of X where

$$EX_{ji} = \frac{\sum_{i=1}^{n} X_{ji} \times (X_{ji} + X_{ki})}{\sum_{i=1}^{n} X_{ji} + \sum_{i=1}^{n} X_{ki}}.$$

To calculate the index of affinity directly from percentage data the lowest value for each species is summed over all species in the two samples, whereas to calculate the city block metric the difference between the two values for a given species is summed.

i.e.

species	sample *j*	sample *k*	% in common I.A.	% difference C.B.
A	20	15	15	5
B	8	17	8	9
C	43	19	19	24
D	24	31	24	7
E	5	18	5	13
Total	100	100	71	58

$$\text{I.A.} = (100 - \tfrac{1}{2}\text{C.B.}) = (100 - \tfrac{1}{2} \times 58) \times 71$$

In order to compare the values of the index of affinity with values of chi-square it was necessary to express chi-square within the range 0–100. This was done using an extension of Pearson's coefficient of contingency as follows:

$$C = \left(\frac{\chi^2}{N+\chi^2}\right)^{\frac{1}{2}}.$$

C = coefficient of contingency; $N = n_1 + n_2$, where n_1 = number of identifications in sample 1 and n_2 = number of identifications in sample 2.

Since $0 \leqslant \chi^2 \leqslant N$ (Kendall and Stuart 1967, p. 557) and the index of affinity ranges from 0 to 100, so $0 \leqslant (200 \times C^2) \leqslant 100$ will give a comparable range for an expression linked to C^2. Using the above definitions, a closely similar sample pair will have a high index of affinity and a low coefficient of contingency.

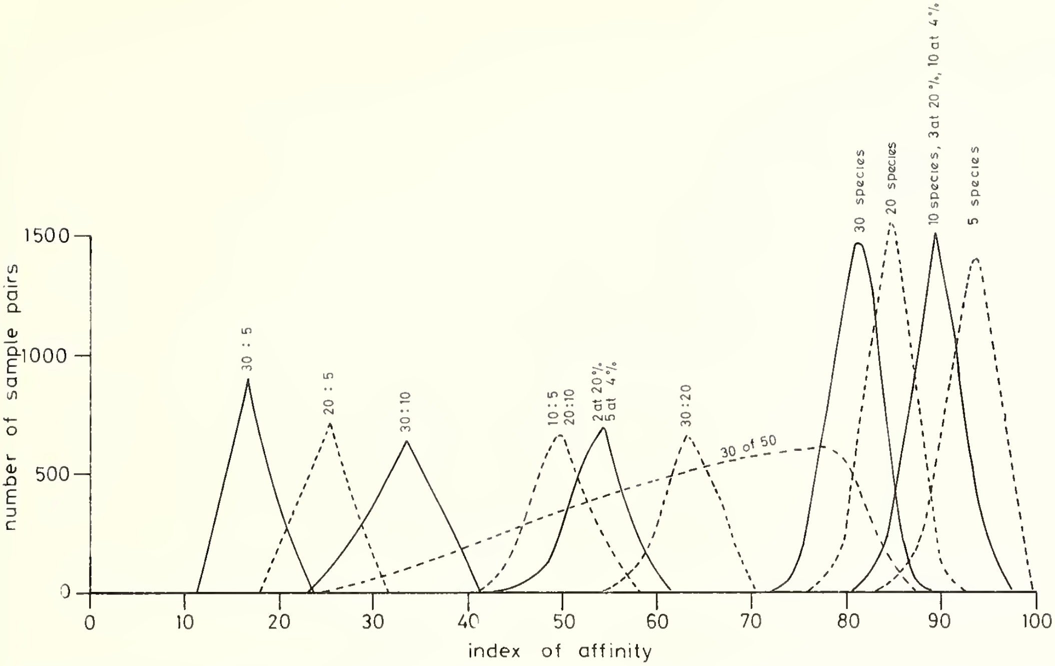
Thus $D = 100\text{–}200C^2$, (D = modified coefficient of contingency) will give values of D which lie within the same range as the values of the index of affinity, high values indicating close similarity of samples. The equations may be rewritten

$$\chi^2 = \frac{ND}{200 - D}$$

whereupon $ND/200 - D$ is distributed approximately as $\chi^2_{(k-1)}$ where k = number of classes, and thus probability statements may be made using this statistic.

For each group of 100 samples, each sample was compared with every other sample and the similarity index entered in the lower diagonal of a square matrix. The distribution of the values was then recorded. When two types of artificial assemblages were compared, only the distribution of the indices for mixed pairs was considered (i.e. only 2500 pairs, 4950 being found for the 100 samples from one assemblage only). Text-fig. 2 shows the distributions of the index of affinity. Text-fig. 3 shows the distribution of the modified coefficient of contingency.

Cluster analysis was not applied to samples taken from the artificial assemblages but it was performed on samples from natural assemblages. The method used was as follows. The two samples which gave the highest index of affinity in the affinity matrix were placed in the first group. An average sample was formed for this group

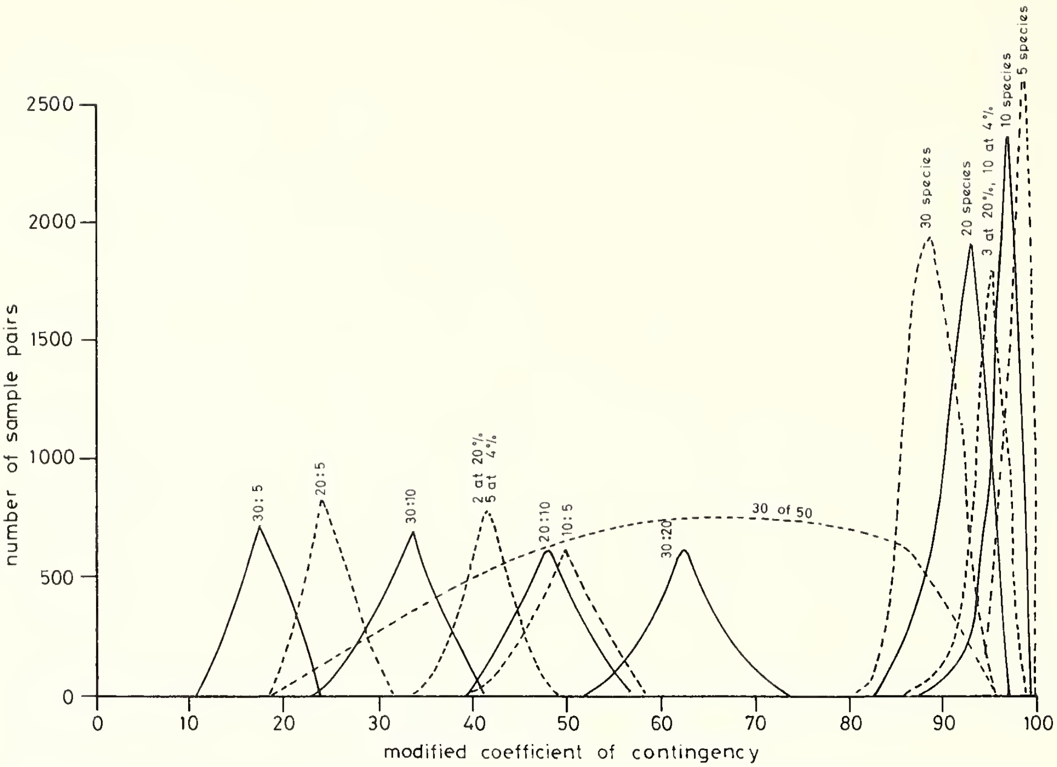


TEXT-FIG. 2. Curves showing the frequency distribution of the index of affinity for sample pairs in artificial assemblages. The numbers at the peak of each curve indicate the number of species in the assemblage(s). Unless otherwise indicated, the species are equally abundant in each model.

by calculating the mean percentage abundance for each species present in either or both samples. The average sample was compared with all other samples and the revised indices of affinity were entered in the affinity matrix. The affinity matrix was again searched for the highest value and the sample pair giving this value was either placed in a new group, or, if one sample was an average sample for a group, the other sample was placed in the same group. If a group contained more than two samples, the average percentage abundance for each species in the group was found by adding together the species abundance for all samples in the group and dividing by the number of samples in the group. In other words, the average sample was an unweighted sample since all samples in the group were equally important in working out the average sample.

ANALYSIS OF RESULTS

When text-figs. 2 and 3 are compared, it is found that the frequency distributions for the index of affinity are very similar to those for the modified coefficient of contingency. The chief difference lies in the curves for models where all the random samples are from the same artificial assemblage. The distribution in the case of the index of affinity is both lower in value and wider in range than is the distribution of the modified coefficient of contingency. When samples are taken from two artificial assemblages the frequency curves of the two measures of similarity are in general



TEXT-FIG. 3. Curves showing the frequency distribution of the modified coefficient of contingency (*D*) for sample pairs in artificial assemblages. The numbers at the peak of each curve indicate the number of species in the assemblage(s). Unless otherwise indicated, the species are equally abundant in each model.

identical. The differences which occur are due to the fact that a squared term occurs in the calculation of the modified coefficient of contingency, and this lowers the value of this coefficient when large numbers of 'species' are present in low abundance. Thus, when samples containing two species at 20% and five species at 4% are compared, the calculation for the coefficient of contingency involves comparing three species at 20% and fifteen at 4%. Thus the value of χ^2 is high because $(X-EX)^2/EX$ is high when EX is small, and $(X-EX)^2/EX$ is evaluated fifteen times for low values of $EX(EX=4\%)$ (where $X=$ observed value and $EX=$ the expected value). Although the curves are not the same for the two similarity indices under discussion, their differences may in general be predicted.

Having established that the index of affinity is a reliable indicator of similarity, let us look more closely at the distribution. Table 1 shows the range and peak of the frequency distribution curve for 95% of the sample pairs in each model. (The remaining 5% of the sample pairs have an index of affinity outside the range noted.)

For each model, the range is, approximately, 10. In the case of single assemblage models, the peak lies at about $(100-Y\times S)$ where S is the number of species. Y is a number whose value is dependent on the value of S. Y is roughly equal to one, but is more precisely a little greater than one when few 'species' are represented and slightly less than one when more than ten species are involved.

In the models where two types of assemblage are compared, the value of the peak of the frequency distribution curve is usually found to be the value which would be obtained if each sample in a sample pair was an accurate representation of the artificial assemblage. Thus, if one series of samples contains five species, each at 20%, and the second series of samples contains thirty species, each at $3\frac{1}{3}\%$, the value of the index of affinity, if each sample is an exact replica of the model, would be $5 \times 3\frac{1}{3}$, i.e. $16\frac{2}{3}$. However, in the models for twenty *v.* thirty species and for two at 20% and five at 4%, the peak of the frequency distribution curves are found to be a little below the expected value—63 instead of 66 for twenty *v.* thirty species and 54 instead of 60 for two at 20% and five at 4%. Thus, if samples with large numbers of species are being compared, we may assume that similarity is implied when a rather lower value than expected is obtained.

TABLE 1. The value of the index of affinity for each model sample.

Number of species in model	Lower	Peak	Upper	Range	Expected peak
5 species	88	94	97	9	
10 species	83	89	94	11	
20 species	80	84	88	8	
30 species	74	81	86	12	
3 at 20%, 10 at 4%	82	88	94	12	
30:5	12	17	21	9	$16\frac{2}{3}$
20:5	20	26	29	9	25
10:5	44	50	56	12	50
20:10	44	50	56	12	50
30:10	27	$33\frac{1}{3}$	39	12	$33\frac{1}{3}$
30:20	58	63	68	10	$66\frac{2}{3}$
2 at 20%, 5 at 4%	48	54	59	11	60

Table 1 summarizes these results; note that the upper and lower $2\frac{1}{2}\%$ of the range of frequency distribution has been cut off, because those sample pairs are considered to be rather extreme.

If sample pairs from assemblages containing only five species have an index of affinity of 90 or more, we see from text-fig. 2 that this is well within the range of distribution expected for a five species example. In the case of the sample pairs (each containing about five species) taken by Buzas (1965) referred to earlier, the index of affinity for pairs of sample assemblages containing more than 100 individuals was usually 89 or greater, and we assume they were from the same assemblage. If we examine the two sample pairs giving values of less than 89, we find that one (Buzas's living, 10, 10′) was from a transitional zone where rapid changes may be expected, and the second (total assemblage, 104, 104′) contained only 115 individuals.

The value of the modified coefficient of contingency for each of Buzas's sample pairs is > 95 (except in living 10, 10′) which lies within the range expected for samples of five species.

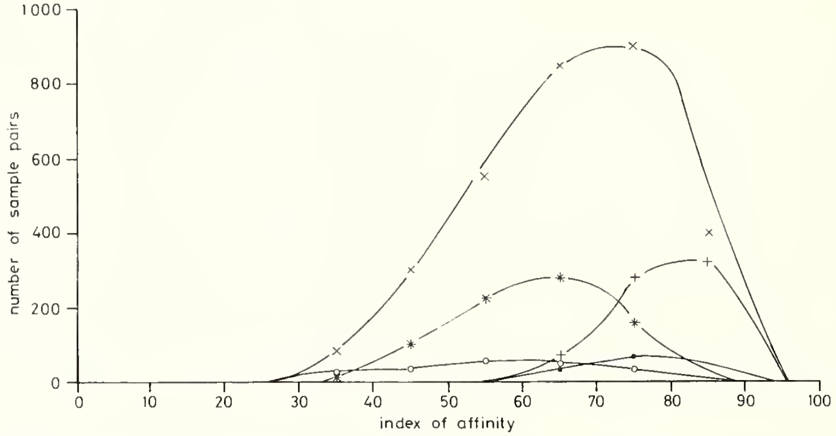
HOLOCENE SEDIMENTS FROM THE WESTERN APPROACHES TO THE ENGLISH CHANNEL

A set of eighty surface and short-core samples of Holocene sediments containing planktonic Foraminifera were taken from the submarine canyon area of the Western Approaches to the English Channel. The water depth ranged from 100 to 2000 fathoms. From each sample the author counted about 250 individuals.

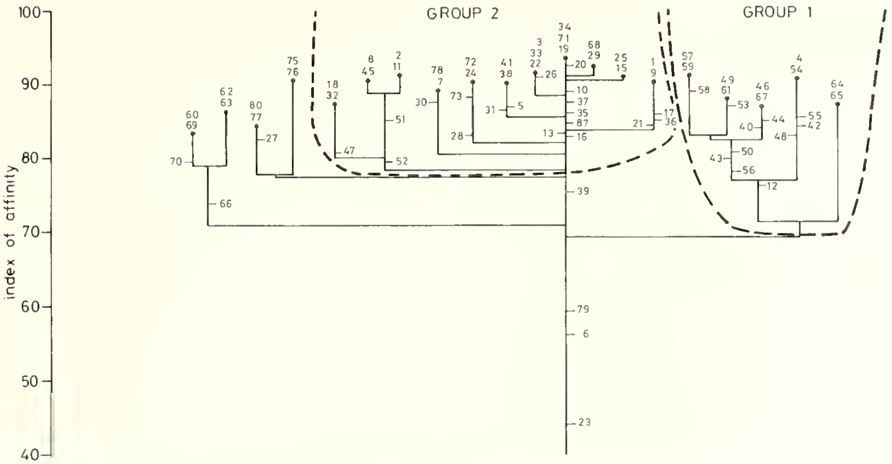
The assemblages were composed generally of about five species at 10–30% abundance and up to ten species at 5%, or, in many cases $< 1\%$ abundance. The range of frequency distributions is from 22 to 95 with a peak at about 70 (see text-fig. 4). If the samples followed the single assemblage model, they should produce a graph similar to the 20- or 10-species model, with a range about 80–95 with a peak of about 87 (see text-fig. 2). Since we are dealing with natural assemblages, lower values for the index of affinity may be accepted to indicate a similar origin for the samples.

In the present case, a range of 74–90 with a peak at 82 would indicate that the samples were from the same assemblage. The Holocene samples differ from this expected distribution because many sample pairs have an index of affinity lower than 75 which suggests that more than one assemblage is being sampled.

A grouping of the samples using the unweighted pair-group method described earlier is shown in text-fig. 5. Ideally, the groups should form above 75 if they contain samples from the same assemblage. Samples 64 and 65 were added to group 1 because they fell naturally near that group. Samples down to 39 could have been included in group 2. Within-group and between-group frequency distribution curves are shown for groups 1 and 2 (text-fig. 4). The within-group range for both groups is from 55 to 90, but the peak for group 2 is higher (about 82) than for group 1 (about 75) which indicates that group 1 is less homogeneous than group 2. The



TEXT-FIG. 4. Curves showing the frequency distribution of the index of affinity for planktonic Foraminifera from the Western Approaches. × = all samples; ● = group 1; + = group 2; ○ = ungrouped samples; * = group 1 compared with group 2.

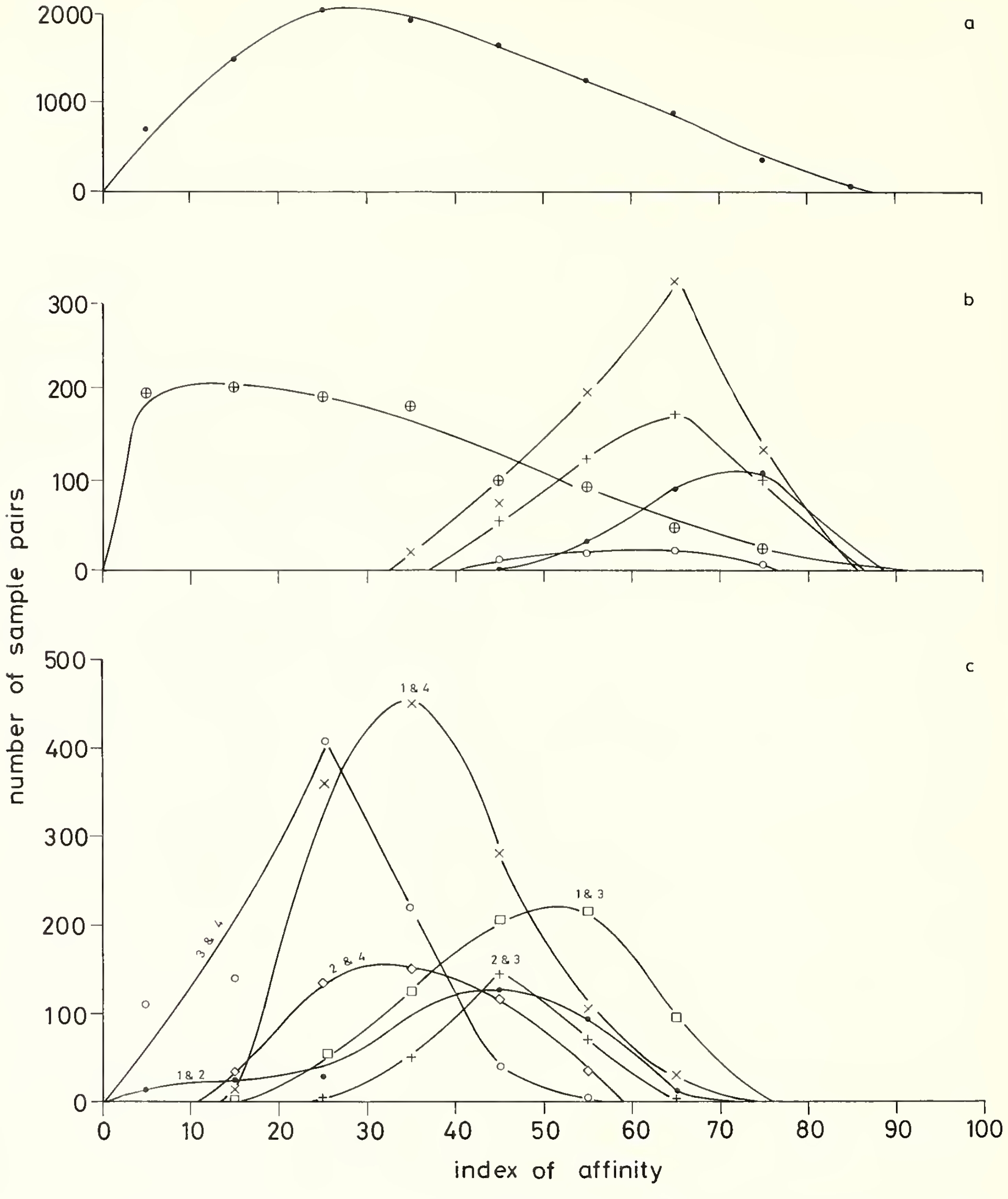


TEXT-FIG. 5. Grouping of Holocene samples of planktonic Foraminifera from the Western Approaches to the English Channel.

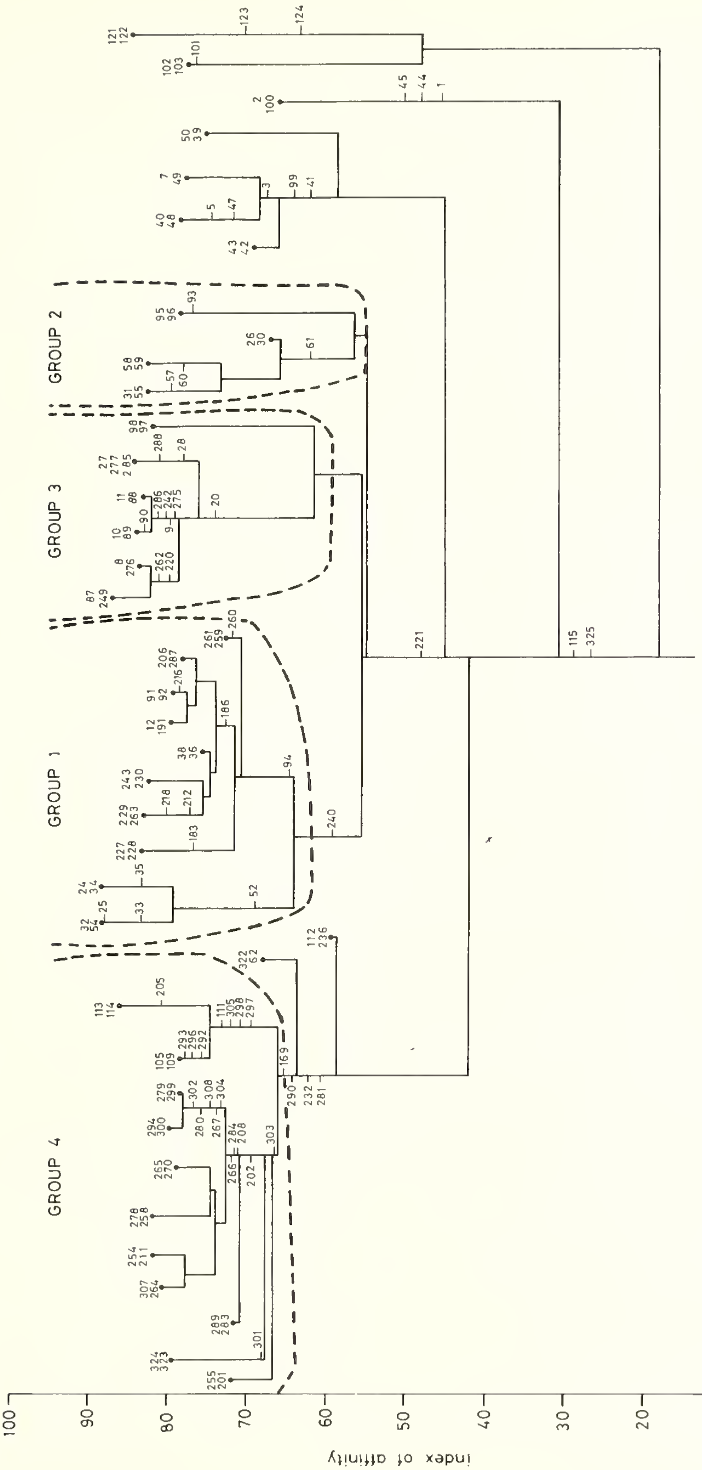
between-group curve shows a wider range (35–90) with a peak at 65 which suggests that the two groups are only moderately similar. The ungrouped samples have little in common with each other since the index of affinity for most sample pairs is less than 75.

SAMPLES FROM THE CALIFORNIAN SEABOARD

Uchio (1960) analysed 154 samples of benthonic Foraminifera from the Californian seaboard, depths of the samples ranging from 0 to 600 fathoms. Up to sixty species were present in the dead (total) assemblage for each sample studied and at least 100 specimens were counted. Five species were predominant, others often occurring at < 1% abundance. As the assemblages lived on the sea floor, differences may well be found in neighbouring samples because of minor differences in the environment and because benthonic forms are usually patchily distributed. Thus, two samples which represent essentially the same environment may have two dominant species in common, but each may have an additional third dominant species not found in the other sample (see figs. 95, 96 in Murray 1973). Looking at the frequency distributions for the artificial assemblages, one might expect samples from the Californian seaboard to show a distribution similar to the 2 at 20%, 5 at 4% curve, or 20 species present out of 30 equally abundant species, i.e. a distribution ranging from 45 to 70 with a peak at about 55. In fact the frequency distribution for the index of affinity for all Uchio's samples ranges from 0 to 88 with a peak at 25 (text-fig. 6*a*). As one might expect, more than one assemblage was sampled. The author grouped the samples by the method indicated earlier, and four main groups were considered to be present (text-fig. 7). The curves of the frequency distribution for within- and between-group indices of affinity were drawn and are shown in text-fig. 6*b*, *c*. In each case the range for the within-group frequency distributions was from 30 to 90 with a peak > 55. The ungrouped samples gave a frequency distribution ranging from 0 to 80 with a peak at about 10.



TEXT-FIG. 6. Curves showing the frequency distribution of the index of affinity for benthonic Foraminifera (total assemblages) from the Californian seaboard (Uchio 1960). *a*, all samples compared with each other. *b*, within-group comparison of groups 1-4 and ungrouped samples. ○ = ungrouped samples; + = group 1; o = group 2; ● = group 3; × = group 4. *c*, groups 1-4 compared with each other.



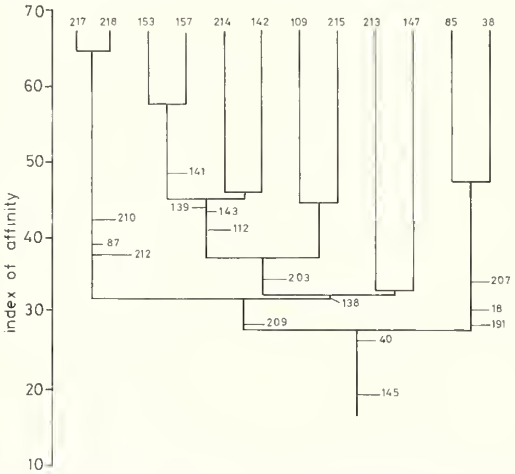
TEXT-FIG. 7. Grouping of samples of benthonic Foraminifera (total assemblages) from the Californian seaboard (Uchio 1960).

The between-group frequency distributions (text-fig. 6*c*) have a much lower peak —25 for groups 3 and 4, 55 (the highest between-group peak) for groups 1 and 3, which we considered to be most closely related in the clustering.

When these groups were compared with Uchio's depth zones, group 4 contained samples only from fauna 4 and indeed all the fauna 4 samples with the inclusion of sample 62 could have been grouped together. The fine-sand and coarse-sand distinctions were found and these two faunas were not linked. Uchio's faunas 2 and 3 were not revealed when the index of affinity was used for grouping. Group 2 corresponds to the deeper samples from the Loma Sea Valley and northern samples from 20 to 60 fathoms form a group that is not numbered. Group 3 contains most of the remaining samples from less than 100 fathoms and group 1 samples are in general from 100 to 200 fathoms.

LIVING BENTHONIC FORAMINIFERA FROM THE GULF OF CALIFORNIA

Phleger (1964) described seventy-six samples of living benthonic Foraminifera from the Gulf of California. Of these only twenty-seven samples contained > 100 foraminiferids. Ten to thirty species were recognized in each sample, about four species being > 10% abundant. The composition of the sample assemblages is thus similar to those described by Uchio and if samples were drawn from the same benthonic assemblage the index of affinity should range again from about 45 to 70 with a peak about 55. In fact, when the frequency distribution of the index of affinity is calculated for the twenty-seven samples containing 100 specimens or more it is found that the range is 0–65 with a peak between 10 and 20. Only twenty-two sample pairs have an index of affinity > 40. This suggests that a wide variety of foraminiferal assemblages are present in the Gulf of California and Phleger did not get many samples from the same assemblage. Using Q-mode (sample/sample) factor analysis on all seventy-six samples, Streeter (1972) recognized nine assemblages and the characteristic species, together with their abundance are given for several of them. Groups obtained using the index of affinity were almost exactly the same as Streeter's groups, both in samples contained and, taking the mean species abundance for each group, in species content. However, only two sample pairs, 218, 217 and 153, 157, seem to represent two natural assemblages (see text-fig. 8) and it is doubtful whether further grouping of these samples adds to our understanding of the distribution of living benthonic Foraminifera in the Gulf of California.



TEXT-FIG. 8. Grouping of samples of living benthonic Foraminifera from the Gulf of California (Phleger 1964).

In recent years many numerical methods have been used to try to group natural assemblages and in most cases the results support and amplify traditional techniques. The index of affinity would seem to be as effective as more complex methods and takes about a quarter of the time to compute as the complex methods. It may equally well be applied to small or large data sets. The range indicating that samples are from the same natural assemblage varies with the number of species present in quite a simple manner. It has been used here on modern and Holocene assemblages where the environment is known, but it should be possible to apply it to older fossil assemblages.

Acknowledgements. The author thanks Dr. P. J. Clifford and Dr. J. K. Ord for useful discussions on statistical problems and Professor J. W. Murray for much helpful criticism. Mr. D. Hamilton kindly made available the samples of Holocene sediment from the Western Approaches. The numerical work was done on the ICL 4-75 computer at Bristol University using the programming language AlgolW. A Computer Centre Library Procedure was used to generate the pseudo-random numbers.

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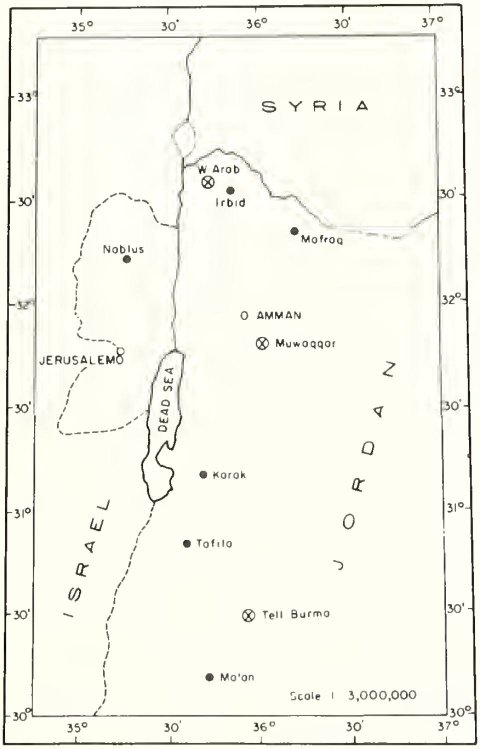
LATE MESOZOIC AND EARLY CAINOZOIC BENTHIC FORAMINIFERA FROM JORDAN

by A. I. FUTYAN

ABSTRACT. Foraminiferal faunas from the Late Mesozoic–Early Cainozoic succession in three widely separated surface sections in Jordan are studied in detail. The benthic and planktic foraminifera have been used to interpret the stratigraphy. The Mesozoic–Cainozoic boundary is marked by distinct lithological and microfaunal changes; there is also a hiatus between the Middle and Late Paleocene. Thirteen new species and one subspecies are described and illustrated.

RESEARCH into the biostratigraphy of the Late Cretaceous (Maastrichtian) and Early Cainozoic (Paleocene and Early Eocene) succession in East Jordan, has resulted in the description and illustration of thirteen species and one subspecies of foraminiferid considered new. The material studied was collected from three surface sections in northern, central, and southern Jordan; at Wadi Arab, Muwaqqar, and Tell Burma respectively (text-fig. 1). The sections and the relative sample



TEXT-FIG. 1. Location map.

[Palaeontology, Vol. 19, Part 3, 1976, pp. 517–537, pls. 81–83.]

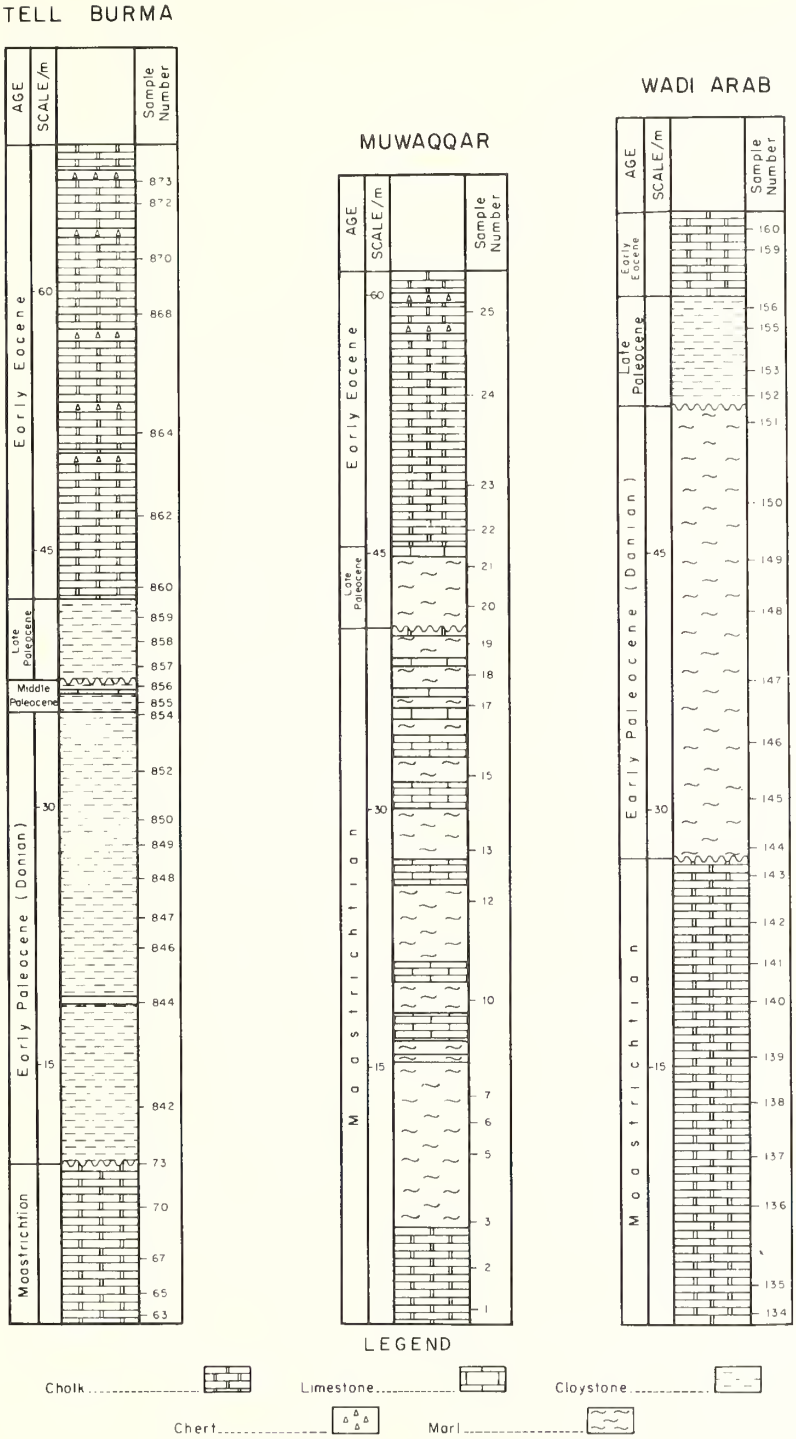
positions are indicated in text-fig. 2. The planktic foraminiferal generic names used are those of Bolli (1957), El-Naggar (1966), and Loeblich and Tappan (1957). New names introduced by Loeblich and Tappan (1964) are regarded here as of subgeneric importance and not used.

BIOSTRATIGRAPHY

This study is based on samples from three previously undescribed widely separated, stratigraphic surface sections of Late Cretaceous–Early Cainozoic age in Jordan. Two hundred and twenty-seven species and subspecies of benthic and planktic foraminifera were recorded and used to establish the stratigraphy. The Cretaceous–Paleocene boundary is an unconformity in all three sections and is marked by a distinct lithological and microfaunal break.

In the Tell Burma section early Middle Paleocene is overlain unconformably by the Late Paleocene. In the Muwaqqar section 4 m of Late Paleocene marls rest directly on Late Maastrichtian chalks and marls while at Wadi Arab Late Paleocene shales overlie Early Paleocene marls. Several benthic species, including *Neoflabellina rugosa leptodisca* (Wedekind), *Praebulimina carseyae* (Plummer), *Spiroplectammina knebeli* LeRoy, *Vaginulina cretacea* Plummer, and the planktics *Globotruncana gansseri* Bolli, and *G. lugeoni* Bolli, disappear above sample 68 in Tell Burma, 141 in Wadi Arab, and 3 in the Muwaqqar section (text-fig. 2). Several other species such as *Gavelinopsis baylissi* sp. nov., *Hopkinsina arabina* sp. nov., and *Vaginulinopsis directa* (Cushman) first appear in the samples above accompanied by a sudden abundance of *Globotruncana esnehensis* Nakkady and *G. stuartiformis* Pessagno. This characteristic fauna enables two subzones to be established. These represent the Middle and Late Maastrichtian in the three sections. Both the Middle Maastrichtian benthic and planktic assemblages include species which occur in the Middle Maastrichtian Cr3c Zone in the Netherlands and Belgium and the Middle Maastrichtian *G. gansseri* Zone in Egypt (El-Naggar 1966) and Trinidad (Bolli 1959, 1966). The appearance of several new species in the sequence overlying the Middle Maastrichtian, their very short ranges, and the relative abundance of *G. esnehensis* Nakkady, which characterizes the Late Maastrichtian in Egypt (El-Naggar 1966), indicates that this part of the section at all three localities is of Late Maastrichtian age. The interval comprising samples 842–847 at Tell Burma is considered to be Middle Danian on the following evidence:

1. Certain species described by Pozaryska (1965) from the Middle Danian, Bryozoan limestone of Stevns Klint and from zones II and III of Wind, Danske Kalk of Denmark (Hofker 1966), are present, these include the benthics *Allomorphina paleocenica* Cushman, *Anomalinoides acuta* (Plummer), *A. danicus* Brotzen, *Guttulina problema* d'Orbigny, *Karreriella fallax* Rzehak, and *Lenticulina spissocostata* (Cushman) and the two planktic species *Globigerina triloculinoides* Plummer and *Globorotalia pseudobulloides* (Plummer).
2. *Globigerina daubjergensis* Brönnimann and *Globorotalia compressa* (Plummer) which, according to Troelsen (1957), occur abundantly in the highest type Danian, are very rare or absent at Tell Burma.



TEXT-FIG. 2. Lithological logs and sample locations.

3. Type Danian foraminifera include species such as *Alabamina midwayensis* Brotzen, *Chiloguembelina morsei* Kline, *Loxostomoides applinae* (Plummer), and *Pulsiphonina prima* (Plummer) which occur in the upper part of the Danian sequence, Hofker (1966), Pozaryska (1965). They do not appear in the Tell Burma section below sample 848.

At Tell Burma the interval from sample 848 to 854 and from 144 to 151 in the Wadi Arab section are considered Late Danian in age because several species characteristic of the Late Danian elsewhere, are abundant. These are *Gavelinella limbata* Olsson, *Globigerina daubjergensis* Brönnimann, *Globorotalia compressa* (Plummer), and *Globigerina trinidadensis* Bolli.

At Tell Burma the Late Danian is overlain by strata containing acute-margined globorotalids, in particular *Globorotalia angulata* (White) and *G. uncinata* Bolli. These planktics are accompanied by the following benthics *Chilostomella czjzeki* Reuss, *Gyroidinoides girardana* (Reuss), *G. globosa* (Hagenow), *Lenticulina alabamensis* (Cushman), *L. punctata* (Rzehak), *Martinottiella alabamensis* (Cushman), *Nodosaria robinsoni* sp. nov., and *Siphogenerinoides.* A correlation can be made based on this fauna between this part of the section and the Middle Paleocene *Globorotalia uncinata* Zone of Bolli (1957, 1959, 1966), the Egyptian *G. uncinata* Subzone of El-Naggar (1966), and the lower part of the *Globigerina* and keeled *Globorotalia* Zone of Reiss (1955), Israel.

The Late Paleocene is present in the three sections studied and shows a pronounced faunal change from the underlying Danian or Middle Paleocene. The following diagnostic planktic species were recorded: *Globigerina velascoensis* Cushman, *Globorotalia acuta* Toulmin, *G. aequa* Cushman and Renz, *G. velascoensis* (Cushman), *Alabamina floscellus* (Schwager), *Bulimina serratospina* Finlay, *Clavulina parisiensis* d'Orbigny, *Eouvigerina zealandica* (Finlay), *Pseudonodosaria laevigata* (d'Orbigny), and *Reussella pseudocacumenata* Olsson. These species indicate that the sections can be correlated with the Late Paleocene, *Globorotalia velascoensis* Zone of Bolli (1957, 1959, 1966) and the *G. acuta*/*G. aequa* Zone of Berggren (1963, 1965), Bolli and Cita (1960), El-Naggar (1966), and Olsson (1960).

The Paleocene in the sections is quite distinct both lithologically and faunally from the overlying Early Eocene. Most of the Paleocene species become extinct before the Early Eocene. The Paleocene–Early Eocene boundary has been drawn at the top of the *G. velascoensis* Zone (*G. acuta* Subzone/*G. aequa*) Berggren (1965), Bolli (1957, 1959, 1966), Bolli and Cita (1960), El-Naggar (1966), and Loeblich and Tappan (1957). This is supported by:

1. The complete extinction of certain genera such as *Neoflabellina*, which is known from the Late Cretaceous and Paleocene only.

2. The first appearance of several species known to characterize the Eocene in several parts of the world, e.g. *Clavulinoides triquetra* (Reuss), *Hanzawaia cushmani* (Nuttall), *Lenticulina incisus* (Lys), and *Rectobolivina nuttalli* (Cushman and Siegfus).

3. The first appearance of several Early Eocene planktic species recorded from North America, Europe, and the Middle East, such as *Globigerina soldadoensis* Brönnimann, *Globorotalia formosa gracilis* Bolli, *G. rex* Martin, and *G. wilcoxensis* Cushman and Ponton.

TABLE 1. Stratigraphical distribution of selected benthic foraminiferal species in the Maastrichtian–Early Eocene strata in East Jordan.

Benthic Foraminifera	Maastrichtian		Paleocene			Eocene
	Middle	Late	Early	Middle	Late	Early
Spiroplectammina knebeli LeRoy	× × × × × ×					
Vaginulina cretacea Plummer	× × × × × ×					
Neoflobellino leptodisco (Wedekind)	× × × × × ×					
Vaginulina silicula Plummer	× × × × × ×	× × × × × ×				
Neoflabellino reticulata deltoidea (Marsson)	× × × × × ×	× × × × × ×				
Siphogenerinoides oveyi Nakkady	× × × × × ×	× × × × × ×				
Reussella aegyptiaca Nakkady	× × × × × ×	× × × × × ×				
Bolivina incrassota Reuss	× × × × × ×	× × × × × ×				
Gyroidinoides tellburmaensis sp. nov.	× × × × × ×	× × × × × ×				
Hopkinsina arabina sp. nov.		× × × × × ×				
Govelinopsis baylissi sp. nov.		× × × × × ×				
Alabamina wilcoxensis limbata (Plummer)			× × ×			
Cibicidoides felix (Martin)			× × ×			
Angulogavelinella bandato sp. nov.			× × ×			
Clavulina barnardi sp. nov.			× × × × × ×			
Marginulinopsis eocaenicus (Franke)			× × × × × ×			
Frondiculorio midwayensis Cushman			× × × × × ×			
Valvulineria duwi (Nakkady)			× × × × × ×	× × × × × ×	× × × × × ×	
Marginulina jordanensis sp. nov.			× × ×			
Gavelinello limbata Olsson			× × ×			
Frondicularia nokkodyi sp. nov.			× × ×	× × × × × ×	× × × × × ×	
Loxostomoides applinae (Plummer)			× × ×	× × × × × ×	× × × × × ×	
Pulsiphonia prima (Plummer)			× × ×	× × × × × ×	× × × × × ×	
Martinottiello olabamensis (Cushman)				× × × × × ×		
Nodosaria robinsoni sp. nov.				× × × × × ×		
Siphogenerinoides elnaggari sp. nov.				× × × × × ×	× × ×	
Quadrimorphino esnehensis (Nakkady)				× × ×	× × × × · ·	
Clavulina parisiensis d'Orbigny					× × × × × ×	
Voginulinopsis wadiarabensis sp. nov.					× × × × × ×	
Frondiculario pickeringi sp. nov.					× × × × × ×	
Palmula woodi Nakkady					× × × × × ×	
Eouvigerina zealondica (Finlay)					× × × × × ×	
Gaudryina soldadoensis tellburmaensis subsp. nov.					× × ×	× × × × × ×
Lenticulina incisus Lys.						× × × × × ×
Eouvigerina iranica (Thomas)						× × × × × ×
Reussello truncanella (Finlay)						× × × × × ×
Rectobolivina nuttalli (Cushman and Siegfus)						× × × × × ×
Bulimina leroyi sp. nov.						× × × × × ×
Valvulinaria pseudotumeyensis sp. nov.						× × × × × ×
Hanzawaia cushmani (Nuttall)						× × × × × ×
Clavulinoides cf. *depressa* (Cushman and Ellisor)						× × ×
Clavulinoides triquetra (Reuss)						× × ×

SYSTEMATIC PALAEONTOLOGY

Genus GAUDRYINA d'Orbigny in de Sagra 1839

Gaudryina soldadoensis tellburmaensis subsp. nov.

Plate 81, figs. 1, 2

Holotype. BMNH. P49102.

Type locality and horizon. Tell Burma, southern Jordan, Early Eocene, sample 862.

Dimensions of holotype in mm. Length 1·1; maximum width 0·45; thickness 0·25.

Derivation of name. After the type locality.

Material. Sixteen specimens from four samples. This subspecies appears in the Late Paleocene of the Tell Burma section and ranges to the Early Eocene.

Diagnosis. Test triserial with pyramidal initial portion followed by inflated chambers semicircular in cross-section separated by deeply depressed sutures. Inflated chambers slightly indented.

Description. Test elongate with a pyramidal, triserial early portion forming about one-third of test. This is followed by the biserial portion which comprises semicircular chambers in cross-section. Chambers of triserial portion are indistinct while the biserial portion has six to eight clearly defined inflated chambers. Sutures indistinct in triserial portion; deeply depressed forming marked indentations throughout biserial portion. Wall very finely arenaceous, smooth with calcite cement. Aperture rounded with a thickened margin near the inner edge of the last-formed chamber, showing tendency to become terminal.

Remarks. Subspecies differs from the nominate species in having inflated biserial chambers and in being triangular in cross-section in the triserial and circular in the biserial parts. As in the nominate species, aperture rounded with thickened margin near the inner edge of last-formed chamber, showing tendency to become terminal; in this respect the subspecies approaches the genus *Bermudezina*. *Gaudryina laevigata* Franke var. *saadi* Haque (1956) from the Early Eocene of West Pakistan is similar in shape, but the biserial portion is rounded quadrangular in cross-section.

Genus CLAVULINA d'Orbigny, 1826

Clavulina barnardi sp. nov.

Plate 81, figs. 3, 4

Holotype. BMNH. P49101.

Type locality and horizon. Tell Burma, southern Jordan, Danian, sample 852.

Dimensions of holotype in mm. Length 1·0; width 0·17.

Derivation of name. After Professor T. Barnard, University College, London.

Material. Forty-two specimens from six samples. *Clavulina barnardi* sp. nov., is a good Danian index fossil in the Tell Burma and Wadi Arab sections.

Diagnosis. A slender *Clavulina* with sharply pyramidal, triserial portion followed by slightly irregular flask-shaped, inflated, uniserial chambers. Sutures deeply excavated.

EXPLANATION OF PLATE 81

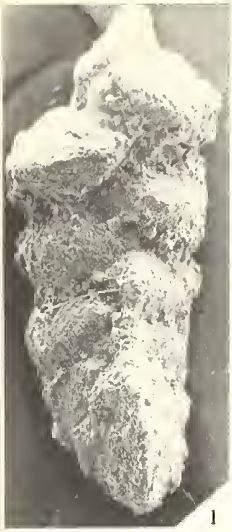
Figs. 1, 2. *Gaudryina soldadoensis tellburmaensis* subsp. nov. 1, 2, holotype, sample 862, Tell Burma section; 1, frontal view, ×63; 2, side view, ×65.

Figs. 3, 4. *Clavulina barnardi* sp. nov. 3, holotype, sample 852, Tell Burma section, ×65; 4, paratype, sample 852, Tell Burma section, ×60.

Figs. 5, 6. *Marginulina jordanensis* sp. nov. 5, holotype, sample 849, Tell Burma section, frontal view, ×36; 6, paratype, sample 849, Tell Burma section, side view, ×36.

Figs. 7–9. *Vaginulinopsis wadiarabensis* sp. nov. 8, 9, holotype, sample 156, Wadi Arab section; 8, frontal view, ×38; 9, side view, ×38; 7, paratype, sample 858, Tell Burma section, frontal view, ×43.

Figs. 10–12. *Gyroidinoides tellburmaensis* sp. nov. 10–12, holotype, sample 65, Tell Burma section, ×100; 10, umbilical view; 11, side view; 12, spiral view.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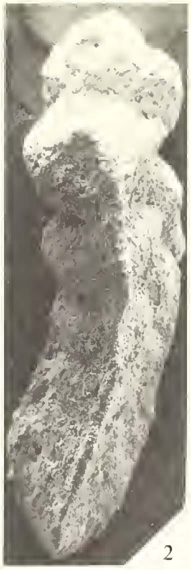
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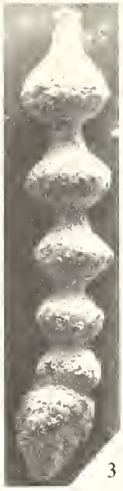
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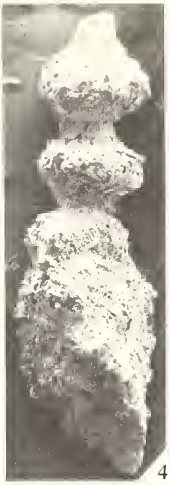
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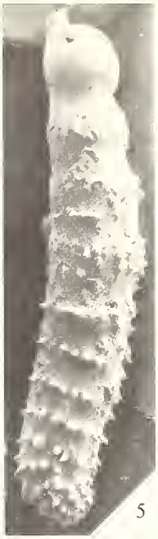
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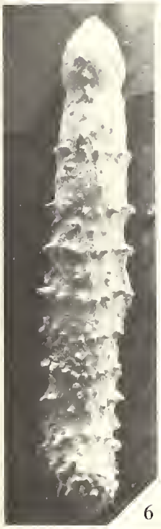
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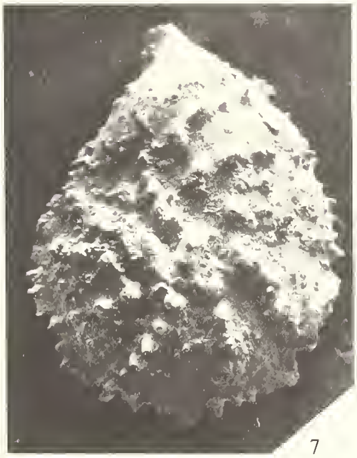
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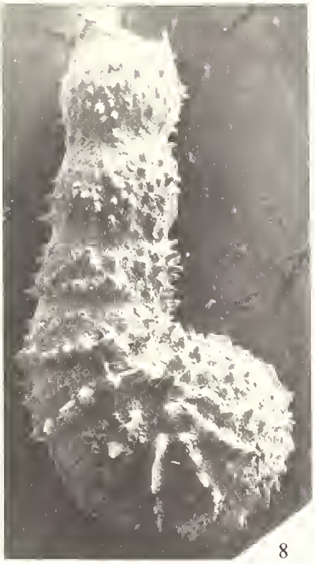
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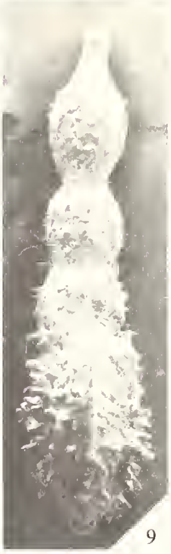
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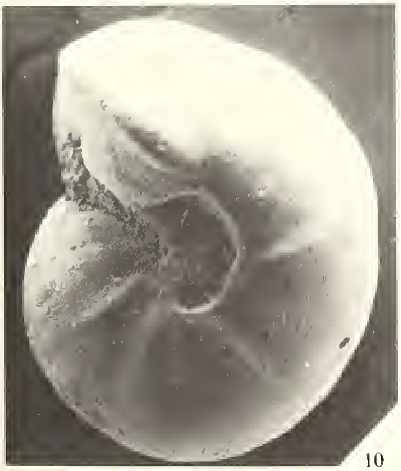
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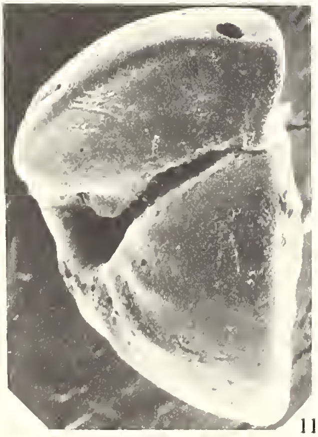
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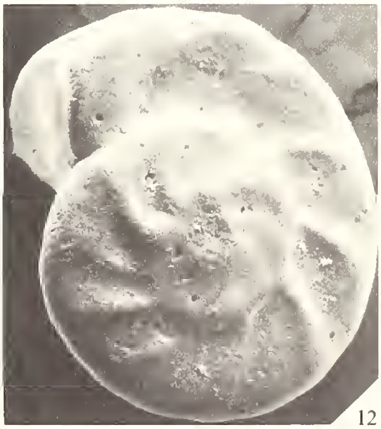
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FUTYAN, Foraminifera from Jordan

Description. Test elongate, early portion triserial and sharply pyramidal with acute apical end comprising about one-fifth to one-half of entire test. The uniserial portion consists of three to eight flask-shaped inflated chambers, with subacute to rounded profiles in longitudinal section. The sutures are indistinct in triserial portion, deeply excavated in uniserial portion. Wall finely arenacous with calcite cement and with rough surface. Aperture rounded terminal at end of tubular neck. Microspheric generation has slender test, smaller, initial, triserial portion and larger number of uniserial chambers than megalospheric generation.

Remarks. The test varies widely in both size of the initial triserial portion which may comprise one-fifth to one-half of the test and number of uniserial chambers which may be three to eight.

This species is similar to *Pseudoclavulina globulifera* Ten Dam and Sigal (1950), but differs in having a triserial, sharply pyramidal early portion and uniserial chambers with slightly angular or rounded outlines in profile.

Genus VAGINULINOPSIS Silvestri, 1904
Vaginulinopsis wadiarabensis sp. nov.

Plate 81, figs. 7–9

Holotype. BMNH. P49111.

Type locality and horizon. Wadi Arab, near Irbid, northern Jordan, Late Paleocene, sample 156.

Dimensions of holotype in mm. Length 1·85; maximum width 1·0; thickness 0·25.

Derivation of name. After the type locality.

Material. Thirty-five specimens from three samples. This species is restricted to the Late Paleocene at Tell Burma and Wadi Arab.

Diagnosis. Test with large, planispirally coiled, proximal portion having flanged spinose periphery, heavily ornamented surface, and raised sutures with low sharp spines; followed by uniserial portion with inflated chambers, depressed sutures, and surface in part covered by short spines. Final chambers elongate globular, sutures broadly depressed. Aperture terminal with neck.

Description. Compressed, elongate test, early portion consisting of ten or eleven chambers in about two planispiral whorls. Later portion uniserial, comprises one to four inflated chambers. Periphery of planispiral proximal portion flanged with short spinose projections, uniserial chambers are broadly rounded. Chambers indistinct in coiled part obscured by heavy ornament, but distinct and inflated in uniserial portion. Sutures of proximal part limbate, raised and composed of sharply pointed projections, coalescing irregularly near umbo. Sutures broadly depressed in uniserial portion. Surface of chambers covered with short spines. Aperture terminal radiate with short neck.

Remarks. The number of chambers in the uniserial portion of this species vary from one to four. It is heavily ornamented and characterized by a large, coiled initial portion, spinose sutures, periphery, and surface. It resembles *Vaginulinopsis tuberculata* Plummer (1927), which also occurs in the material examined, but has a larger, coiled initial portion, a stouter test, a flanged, spinose periphery and surface, and one to two inflated uniserial chambers. *V. tuberculata*, also has four to six laterally compressed chambers which are longer than high. *V. verruculosa* Martin (1943) from the Lodo Formation, California, has less closely coiled chambers and different ornamentation.

Genus MARGINULINA d'Orbigny, 1826

Marginulina jordanensis sp. nov.

Plate 81, figs. 5, 6

Holotype. BMNH. P49108.

Type locality and horizon. Tell Burma, southern Jordan, Late Danian, sample 849.

Dimensions of holotype in mm. Length 1·9; width 0·4; thickness 0·16.

Derivation of name. After Jordan.

Material. Twenty-three specimens from three samples. Species confined to the Late Danian of the Tell Burma and Wadi Arab sections.

Diagnosis. A *Marginulina* with two or three chambers forming part of an initial whorl, followed by ten to thirteen slightly inflated chambers arranged rectilinearly. Sutures distinct, raised, marked by spinose tubercles. Last two chambers more inflated than preceding ones and separated by deeply depressed sutures.

Description. Test elongate, slightly compressed laterally, slightly curved, and with concave dorsal and convex ventral margins. Periphery broadly rounded. Test has ten to thirteen chambers, initial two or three form part of a whorl followed by linear succession of slightly inflated chambers broader than high. Sutures raised and marked by spinose tubercles. Last two chambers more inflated than preceding ones and separated by deeply depressed smooth sutures. Chamber wall covered by sparse random coarse tubercles. Aperture terminal, dorsal, rounded, radiate with distinct neck.

Remarks. This species resembles *M. wetherelli* Jones, 1854, a form described from the Eocene, London Clay. *M. wetherelli* is more compressed, with larger initial coiled portion and less-inflated chambers. It also lacks the last two inflated chambers with depressed sutures. *M. jordanensis* sp. nov. does not vary significantly.

Genus NODOSARIA Lamark, 1812

Nodosaria robinsoni sp. nov.

Plate 82, figs. 5, 6

Holotype. BMNH. P49109.

Type locality and horizon. Tell Burma, southern Jordan, Middle Paleocene sample 856.

Dimensions of holotype in mm. Length 0·8; width 0·3.

Derivation of name. After Dr. E. Robinson, University College, London.

Material. Nineteen specimens from two samples. Several well-preserved specimens occur in the Middle Paleocene sample 856 from Tell Burma. The species seems to be confined to the Middle Paleocene.

Diagnosis. Nodosariid with uniserial, inflated chambers covered by twenty-two to twenty-four closely spaced, fine, longitudinal ribs, which become obsolete on the upper half of the last chamber.

Description. Test elongate, cylindrical or slightly tapering, with three or four strongly inflated, almost globular, chambers. Sutures indistinct and deeply depressed. Ornament consists of twenty-two to twenty-four fine, distinct, very closely spaced ribs extending throughout most of the test becoming obsolete on upper half of last chamber. Aperture terminal, radiate.

Remarks. This species shows slight variation in chamber number ranging from three to five. *Nodosaria robinsoni* sp. nov. differs from *N. limbata* d'Orbigny in having fine, distinct, longitudinal ribs. *N.* (*Dentalina*) *capitata* Boll var. *striatissima* Andreae, 1884 is similar, but larger, with more chambers and an initial spine. Specimens referred by Hillebrandt (1962) to *N. limbata* d'Orbigny, 1840 and by Pozaryska (1965) to *Marginulina* sp., are similar and may belong to this species. These were recorded from the Austrian and Polish Paleocene respectively.

Genus FRONDICULARIA Defrance in d'Orbigny 1826
Frondicularia pickeringi sp. nov.

Plate 82, fig. 2

Holotype. BMNH. P49104.

Type locality and horizon. Tell Burma, southern Jordan, Late Paleocene, sample 858.

Dimensions of holotype in mm. Length 1·5; maximum width 1·1; thickness 0·1.

Derivation of name. After Dr. T. Pickering, former Mining Advisor to N.R.A. Jordan.

Material. Thirty specimens from three samples. Species confined to the Late Paleocene at Tell Burma.

Diagnosis. A *Frondicularia* with large, thin, much compressed test distinctly rhomboidal in outline, periphery truncate in upper half of test, irregular with thin, serrated, transparent keel in lower half. Initial portion ornamented by two to five fine ribs which in some specimens extend towards the aperture.

Description. Test free, large, elongate, longer than broad, thin, compressed. Distinctly rhomboidal in outline, with greatest width towards middle of test. Periphery truncate

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EXPLANATION OF PLATE 82

Fig. 1. *Frondicularia nakkadyi* sp. nov., holotype, sample 858, Tell Burma section, ×30.

Fig. 2. *Frondicularia pickeringi* sp. nov., holotype, sample 858, Tell Burma section, ×45.

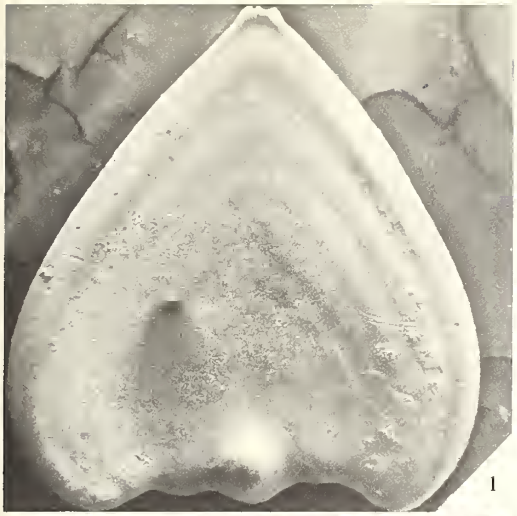
Figs. 3, 4, 10. *Siphogenerinoides elnaggari* sp. nov. 4, 10, holotype, Tell Burma section, sample 857; 4, frontal view, ×140; 10, apertural view, ×225. 3, paratype, Tell Burma section, sample 856, ×150.

Figs. 5, 6. *Nodosaria robinsoni* sp. nov. 5, holotype, Tell Burma section, sample 856, ×87; 6, paratype, Tell Burma section, sample 856, ×82.

Figs. 7–9. *Hopkinsina arabina* sp. nov. 7, 8, holotype, Muwaqqar section, sample 13; 7, apertural view. ×230; 8, frontal view, ×125; 9, paratype, sample 5, Muwaqqar section, ×134.

Figs. 11, 12. *Bulimina leroyi* sp. nov. 11, holotype, Tell Burma section, sample 864, ×132; 12, paratype, Muwaqqar section, sample 23, ×143.

PLATE 82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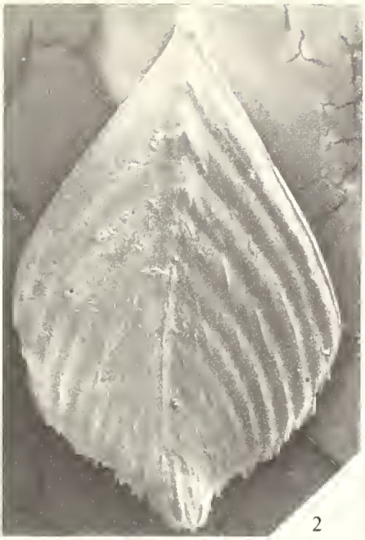
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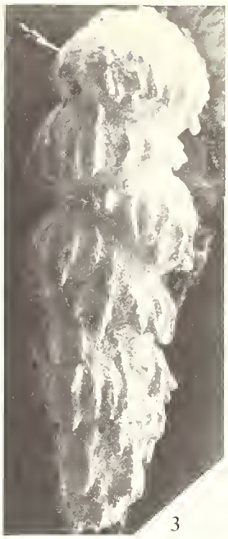
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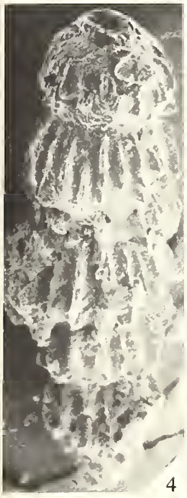
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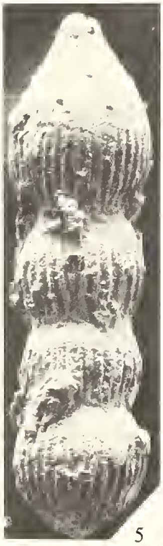
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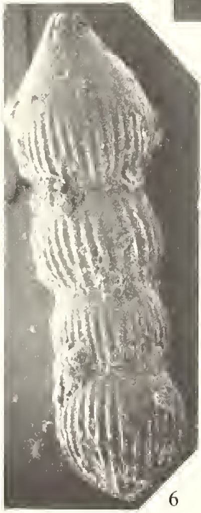
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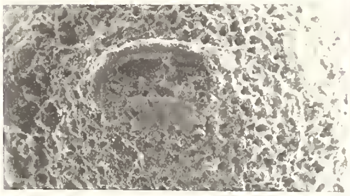
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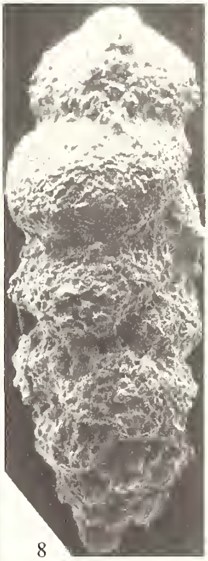
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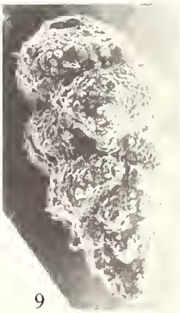
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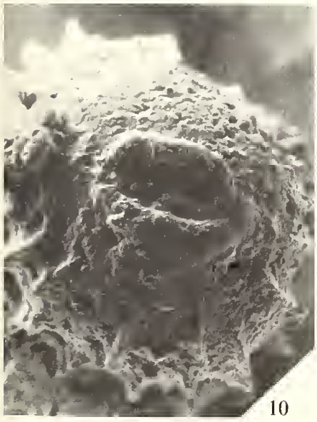
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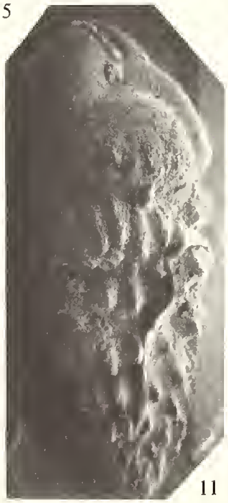
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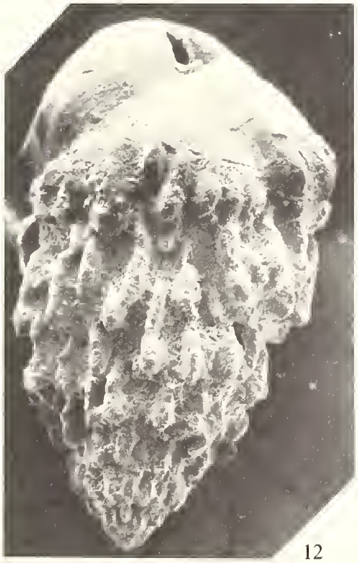
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FUTYAN, Foraminifera from Jordan

in distal part of test, but slightly irregular with thin, serrated, transparent keel and occasional short spines in proximal part. In adult forms there are ten to twelve very narrow, chevron-shaped chambers. Final chamber embraces more than half of test. Initial chambers slightly inflated, gently curved, and ornamented by two to five fine, longitudinal ribs which in some specimens extend towards the aperture. Sutures limbate, hyaline, slightly depressed terminating distally in slightly raised beads which mark the position of successive apertures. Aperture terminal, protruding, and radiate. In some specimens initial portion of test may develop obliquely from the long axis of test, giving rise to a curved initial portion with two to three chambers arranged in part of the whorl.

Remarks. The long fine ribs extending from the initial portion across the test surface are absent in some specimens. The rhomboidal outline, prominent, slightly inflated, ribbed proximal portion, marked consecutive apertures, and serrated margin of proximal half of periphery distinguish this species from other similar forms. *F. pitmani* McLean, 1952 from the Paleocene, Vincentown Formation, New Jersey is similar but has a different outline and long spines near the proloculus. It has a rounded periphery and more inflated initial portion. *Flabellina gahannamensis* Ansary, 1955, from the Late Eocene of Egypt is similar in shape, but has a clearly coiled initial portion with numerous coarse, closely spaced ribs extending right across the surface of the test.

Frondicularia nakkadyi sp. nov.

Plate 82, fig. 1

Holotype. BMNH. P49105.

Type locality and horizon. Tell Burma, southern Jordan, Late Paleocene, sample 858.

Dimensions of holotype in mm. Length 2·3; maximum width 2·4; thickness 0·12.

Derivation of name. After Professor S. E. Nakkady, Assuit University, Egypt.

Material. Seventeen specimens from four samples. The species first appears in the Late Danian at Tell Burma sample 850 continuing as a rare form to the top Palaeocene.

Diagnosis. Test free, large, thin, flat with rounded, triangular outline, periphery truncate, proximal part lobate, surface smooth, chambers strongly embracing, sutures limbate, flush, proloculus slightly inflated.

Description. Test free, large, thin, flat, compressed, very slightly broader than long with greatest breadth near proximal part. Periphery truncate and curved in distal part, truncate and lobate in proximal part. Chambers narrow, ten to thirteen strongly embracing. Sutures distinct, limbate flush or slightly depressed. Proloculus large, globular, surface in proximal part smooth or with two to three faint longitudinal ribs, confined to the initial part of test. Remainder of surface smooth, aperture terminal, radiate.

Remarks. This species is very variable in outline. The broad, proximal part can be straight, undulating or lobed. The area of the proloculus in the megalospheric form is inflated. In some specimens the second and third chambers are broadly curved and embrace the proloculus. The microspheric form has a very small proloculus followed by two to three small, curved chambers. This species differs from *Frondicularia wanneri* Nakkady, 1950, because the central raised ridge which extends from the proloculus to the aperture is absent. *F. palegredensis* Weiss, 1955 from the Peruvian Paleocene is similar in shape, but lacks the broad, lobate proximal peripheral outline of *F. nakkadyi* sp. nov. *F. palegredensis* also has prominent costae over the proloculus, some of which extend along the median line.

Genus SIPHOGENERINOIDES Cushman, 1927
Siphogenerinoides elnaggari sp. nov.

Plate 82, figs. 3, 4, 10

Holotype. BMNH. P49110.

Type locality and horizon. Tell Burma, southern Jordan, Late Paleocene, sample 857.

Dimensions of holotype in mm. Length 0·46; width 0·19.

Derivation of name. After Dr. Z. R. El-Naggar, Kuwait University.

Material. Thirteen specimens from three samples. Recorded from the Middle and Late Paleocene at Tell Burma.

Diagnosis. Initial part triserial, becoming biserial and followed by uniserial, inflated chambers, clearly defined by deeply incised sutures. Chambers ornamented with numerous, plate-like, thin costae, occasionally ending proximally in slightly spinose projections.

Description. Test free, elongate cylindrical except for blunt, slightly tapering proximal part. Chambers in early part of test irregularly triserial in microspheric and biserial in megalospheric generation. Three to five obliquely arranged chambers in distal part inflated and becoming nodosarian. Sutures distinct, deeply incised. Ornament consists of fourteen to sixteen thin, plate-like, longitudinal costae over the whole surface, interrupted by incised sutures and ending proximally in slightly spinose projections. Aperture terminal, elliptical, and bounded by slightly raised rim, connected to preceding apertures by straight tooth plate.

Remarks. This species has probably evolved from *Siphogenerinoides brevispinosa* Cushman, 1939, which appears lower in the sequence, by development of longitudinal costae instead of closely spaced, short spines. In shape and ornament it closely resembles *Siphogenerina mayi* Cushman and Parker, 1931 from the Miocene, Temblor Formation of California. It differs, however, in the shape of the aperture and its internal structure. *Siphogenerinoides elnaggari* sp. nov. does not vary significantly.

Genus HOPKINSINA Howe and Wallace, 1932
Hopkinsina arabina sp. nov.

Plate 82, figs. 7–9

Holotype. BMNH. P49107.

Type locality and horizon. Muwaqqar, near Amman, Maastrichtian, sample 13.

Dimensions of holotype in mm. Length 0·55; maximum width 0·3.

Material. Thirty-five specimens from seven samples. Recorded from the Late Maastrichtian of the three sections.

Diagnosis. Triserial early portion forming one-half of test followed by irregularly triserial chambers which become uniserial. Maximum width at approximately half the length. Sutures deeply depressed, surface of chambers covered by prominent nodes. Chambers compact in proximal portion, inflated, subglobular in distal portion.

Description. Test free, elongate, with greatest width at approximately half the length. Early part triserial, comprising about half the test, followed by irregularly, triserial chambers which become uniserial. Initial part subacute and chambers compact, later becoming distinctly inflated and subglobular. Sutures deeply depressed; wall coarsely perforate, covered with prominent nodes spaced about three times their diameter apart. Aperture terminal, elliptical, bounded by low but distinct rim.

Remarks. The species varies mainly in the distal part of the test which is irregularly triserial, biserial, or becomes uniserial. *Uvigerina elongata* Brotzen, 1936, is similar in shape to *Hopkinsina arabina* sp. nov., but has smaller nodes confined to the initial part of the test and compressed rather than inflated chambers. *U. hispida* Schwager, 1866 has coarse spines, thickly distributed over the entire test and a distinctly protruding neck.

Genus BULIMINA d'Orbigny, 1826
Bulimina leroyi sp. nov.

Plate 82, figs. 11, 12

Holotype. BMNH. P49099.

Type locality and horizon. Tell Burma, southern Jordan, Early Eocene, sample 864.

Dimensions of holotype in mm. Length 0·5; width 0·4.

Derivation of name. After Professor L. LeRoy.

Material. Forty-five specimens from seven samples. Common in the Tell Burma Early Eocene but rare in the Muwaqqar Early Eocene.

Diagnosis. Test elongate, slightly tapering, greatest width at distal end, covered by coarse, closely spaced, plate-like, longitudinal costae. Upper part of last whorl smooth and finely perforate. Chambers roughly rectangular in shape, two to two and one-half times broader than long.

Description. Test elongate, slightly tapering, longer than broad, greatest width at distal end. Chambers distinct, slightly inflated, two to two and one-half times broader than long, roughly rectangular in shape, arranged triserially. Sutures distinctly depressed. Wall, except for the distal part of the last chamber which is smooth and finely perforate, covered by coarse, closely spaced plate-like, longitudinal costae, which are partly interrupted across depressed sutures. Costae more prominent on surface of chambers than across sutures. Aperture long, narrow, terminal on last-formed chamber. Microspheric generation slender with nearly parallel sides, megalospheric form generally stouter with more tapering test.

Remarks. Bulimina microcostata Cushman and Parker, 1936, is similar in shape, but has finer costae and these cover only the lower third of the test. *B. instabilis* Cushman and Parker 1936 is more inflated with irregularly branching costae. *B. leroyi* sp. nov. differs from similar Late Cainozoic forms, such as *B. inflata* Seguenza, 1862 and *B. striata* d'Orbigny, 1843, in having a more elongate, slender test.

Genus VALVULINERIA Cushman, 1926
Valvulineria pseudotumeyensis sp. nov.

Plate 83, figs. 4–6

Holotype. BMNH. P49112.

Type locality and horizon. Tell Burma, southern Jordan, Early Eocene, sample 864.

Dimensions of holotype in mm. Diameter 0·65; thickness 0·25.

Derivation of name. Similar to *Valvulineria tumeyensis.*

Material. Forty-five specimens from four samples. Holotype from the Tell Burma section, where it first appeared in sample 864, 6 m above the Paleocene–Early Eocene boundary. It is common in the Early Eocene at Muwaqqar and Wadi Arab.

Diagnosis. Test free, about equally biconvex, trochospiral, with coarsely perforate wall and raised limbate sutures on spiral and umbilical surfaces. Sutures thickened and strongly elevated towards pole on spiral side but less pronounced on umbilical side.

Description. Test free, biconvex, trochospiral with almost circular outline. Periphery rounded and nonlobulate but broken by raised sutures. Chambers slightly inflated, nine or ten in last whorl increasing gradually in size as added arranged in about two and one-half whorls all visible on spiral side; only those of last whorl seen on umbilical side. Umbilicus surrounded by thickened imperforate shell material. Last chamber has wide imperforate apertural face visible on umbilical side. Sutures thickened and strongly elevated; those on spiral side of last whorl continue on to the umbilical side, where they coalesce around the umbilicus. Sutures curved on spiral surface, straight and radiate on umbilical side, becoming much thicker towards pole on spiral side and umbilicus on umbilical side. Wall coarsely perforate. Aperture arched, umbilical-extraumbilical, opening into umbilical cavity, with narrow lip.

Remarks. Sutures between last two chambers in some specimens are limbate and flush with surface. Spiral suture on spiral side occasionally thickened and irregular, concealing previous whorls. This species is similar in size and morphology to *V. tumeyensis* Cushman and Simonson, 1944, reported from the Late Eocene–Oligocene, Tumey Formation, California. It differs, however, in having thick, strongly raised sutures on both sides of the test and an umbilicus bounded by thickened shell material. *Eponides elevatus* (*Truncatulina elevata* Plummer, 1926) is also similar in shape, but much smaller (half the diameter), has a subconical test and an angular periphery.

Genus GYROIDINOIDES Brotzen, 1942
Gyroidinoides tellburmaensis sp. nov.

Plate 81, figs. 10–12

Holotype. BMNH. P49106.

Type locality and horizon. Tell Burma, southern Jordan, Maastrichtian, sample 65.

Dimensions of holotype in mm. Diameter 0·6; thickness 0·25.

Derivation of name. After the type locality.

Material. Fifty specimens from eight samples. Found in the Maastrichtian of all three sections.

Diagnosis. Test free, planoconvex, trochospiral, flat spiral side, strongly convex, umbilical side, deep, open umbilicus, angular periphery and limbate, slightly raised sutures.

Description. Test free, planoconvex, with flattened or very slightly concave spiral side. Umbilical side strongly convex with moderately large, deep, open umbilicus and high, flattened, apertural face aligned at right angles to previous whorl. Three to three and one-half visible whorls on spiral side. Periphery sharply angular, slightly raised above flat surface of spiral side particularly on last two to three chambers. Nine to ten chambers visible in last whorl. Sutures limbate, oblique, slightly curved on spiral side, straight, radiate on umbilical side, also slightly raised on spiral side especially on early whorls, but flush on umbilical side. In some specimens sutures slightly depressed between last two chambers on both sides. Wall is smooth, very finely perforate. Aperture, a long, narrow slit at base of broad, flattened, apertural face, extending from periphery to umbilicus and with thin apertural flap which widens towards the umbilicus.

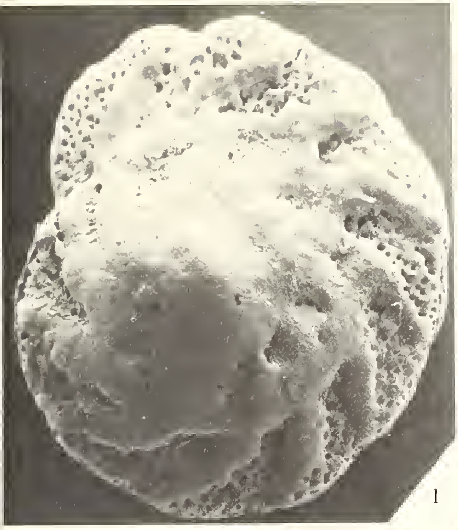
Remarks. This species, when compared with *Gyroidinoides subangulata* (Plummer) 1926 from the Paleocene Midway Formation in the U.S. Gulf Coast area is much larger, has a more acute periphery, more whorls, wider umbilicus and limbate sutures on the spiral side. *G. girardana* (Reuss) 1851 which also occurs in the material studied does not have an angular periphery, raised limbate sutures on the spiral side, but has more inflated chambers. *G. tellburmaensis* sp. nov., does not vary significantly.

EXPLANATION OF PLATE 83

Figs. 1–3. *Angulogavelinella bandata* sp. nov. 1, holotype, sample 846, Tell Burma section, spiral view, ×140. 2, 3, paratype, sample 847, Tell Burma section; 2, side view, ×120; 3, umbilical view, ×120.

Figs. 4–6. *Valvulineria pseudotumeyensis* sp. nov. 4, 5, holotype, sample 864, Tell Burma section; 4, spiral view, ×90; 5, side view, ×90. 6, paratype, sample 23, Muwaqqar section, umbilical view, ×92.

Figs. 7–9. *Gavelinopsis baylissi* sp. nov. 7, 9, holotype, sample 17, Muwaqqar section; 7, spiral view, ×118; 9, umbilical view, ×120. 8, paratype, sample 17, Muwaqqar section, side view, ×73.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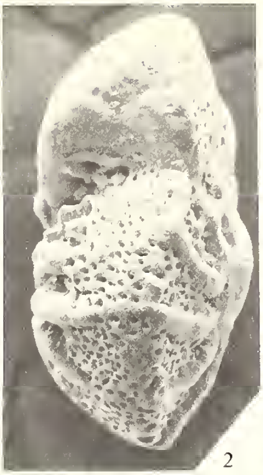
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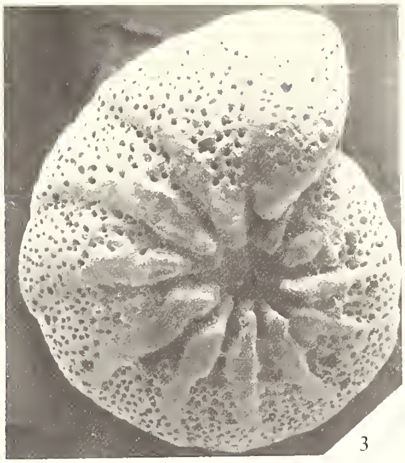
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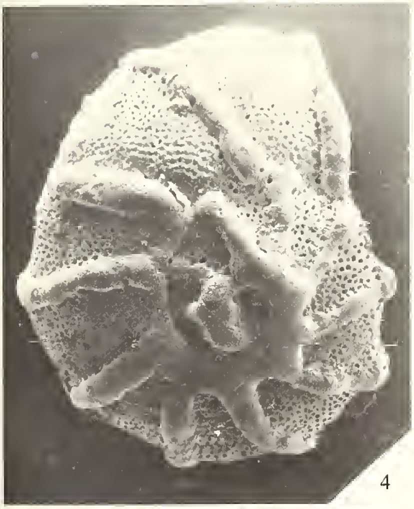
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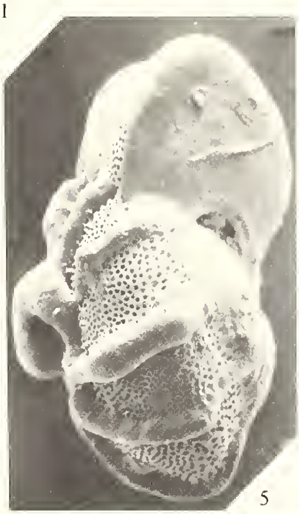
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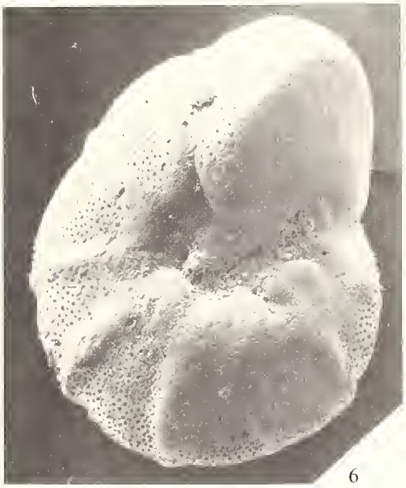
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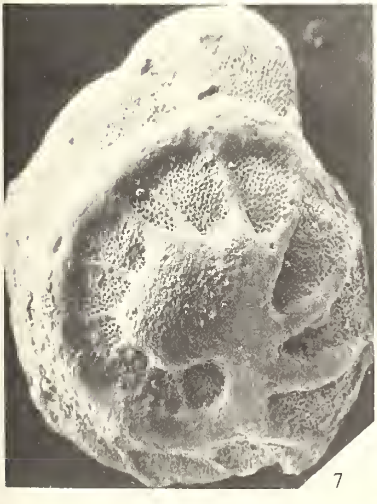
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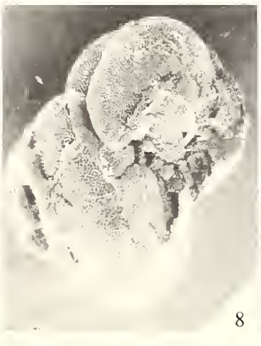
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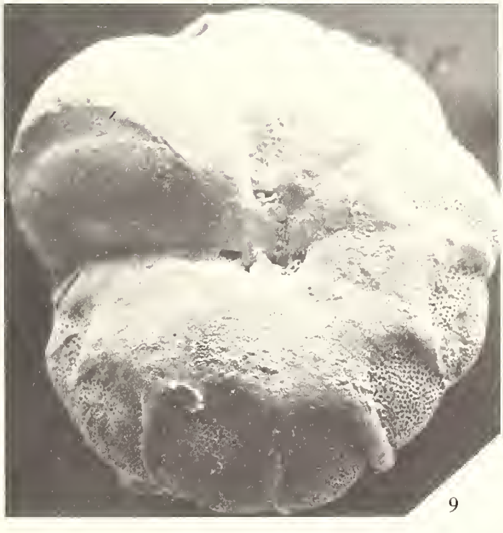
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FUTYAN, Foraminifera from Jordan

Genus ANGULOGAVELINELLA Hofker, 1957
Angulogavelinella bandata sp. nov.

Plate 83, figs. 1–3

Holotype. BMNH. P49098.

Type locality and horizon. Tell Burma, southern Jordan, Middle Danian, sample 846.

Dimensions of holotype in mm. Diameter 0·5; thickness 0·20.

Derivation of name. Based on the type of sutures on the dorsal side.

Material. Thirty-two specimens from three samples. Species found only in the Middle Danian at Tell Burma.

Diagnosis. Test free, unequally biconvex, trochospiral with coarsely perforate wall on both sides; surface of initial whorls raised, covered by thick, milky-white shell material on spiral side. Limbate, raised sutures composed of broad bands of shell material present on both sides of test.

Description. Test free, unequally biconvex, with trochospiral surface of initial whorls raised and last half whorl on spiral side flattened. Umbilical side strongly convex with subacute periphery. Eleven or twelve chambers present in last whorl. Chambers arranged in three to three and one-half whorls partly visible on spiral side. Umbilical side involute with only chambers of last whorl visible. Early whorls on spiral side in most specimens, covered by milky-white shell material. Spiral suture indistinct. Sutures are strongly limbate, broad, raised, and strongly recurved on spiral side composed of bands of milky-white shell material. On umbilical side sutures straight and radiate from an irregular, small umbilical depression. Wall, apart from sutures, coarsely perforate on both sides. Aperture an oblique, elongate slit at base of last chamber midway between periphery and umbilicus. It extends across part of the apertural face and is bounded by a raised rim.

Remarks. Sutures between the last two or three chambers depressed in some specimens, and periphery slightly lobulate. In some specimens sutures are very broad, covering more than two-thirds of the spiral side. *Angulogavelinella bandata* sp. nov. differs from *Pseudovalvulinaria avnimelechi* Reiss, 1952, by having strongly limbate, broad, raised sutures on the spiral side and an open umbilicus.

Genus GAVELINOPSIS Hofker, 1951
Gavelinopsis baylissi sp. nov.

Plate 83, figs. 7–9

Holotype. BMNH. P49103.

Type locality and horizon. Muwaqqar, near Amman, Late Maastrichtian, sample 17.

Dimensions of holotype in mm. Diameter 0·55; thickness 0·22.

Derivation of name. After Dr. D. D. Bayliss to acknowledge his contribution to micropalaeontology in Jordan.

Material. Forty-five specimens from nine samples. Confined to the Late Maastrichtian at Muwaqqar and Wadi Arab.

Diagnosis. Test free, spiroconvex, with high spiral side and slightly convex umbilical side. Spiral and radial sutures prominent, limbate, and raised. Area around umbilicus and first whorl on spiral side covered by imperforate shell material. Wall smooth and finely perforate.

Description. Test free, spiroconvex with very high spiral side. Umbilical side slightly convex. Chambers arranged in high trochospire of about two and one-half whorls all visible on spiral side, inflated chambers nine or ten in last whorl. Only chambers of last whorl visible on umbilical side, but the nine chambers are covered by a thin sheet of imperforate shell material extending from the umbilicus towards the periphery. Umbilicus small but distinct. Spiral suture prominent, limbate, and raised, radial sutures slightly recurved, prominent limbate, and raised on both sides of test, except between last three chambers where they are depressed. The first whorl on spiral side covered by imperforate shell material. Wall smooth, finely perforate, monolamellid, and radial. Aperture, slit extending from near the periphery to the umbilicus at base of broad apertural face.

Remarks. This species varies in the convexity of the umbilical side which is occasionally flattened or slightly convex, as well as in the thickness and extent of thickened imperforate shell material which covers from one-half to two-thirds of the umbilical side and one-fifth to one-third of the spiral side. Koch in 1967 described *Gavelinopsis*(?) *proelevata* from the Early Maastrichtian of Jordan and figured a paratype specimen (pl. 60, fig. 6) which closely resembles this species, but differs from the holotype of *G.*(?) *proelevata* Koch in having a very high spiral side and lacking an umbilical boss. However, *G.*(?) *proelevata* Koch differs from *G. baylissi* sp. nov., in having a more compressed, biconvex test, it has no shell material covering the chambers on the umbilical side and it possesses an umbilical boss. *Valvulineria pseudotumeyensis* sp. nov., is similar in shape, but has a low spiral biconvex test, a more involute spiral side, and an arched aperture with narrow lip opening into the umbilicus.

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FLOW PATTERNS AND DRAG COEFFICIENTS OF CEPHALOPOD SHELLS

by JOHN A. CHAMBERLAIN

ABSTRACT. Streamlining is important in the adaptive strategy of swimmers because it minimizes waste of propulsive energy (i.e. maximizes hydrodynamic efficiency). Streamlining of cephalopod shell form was evaluated by analysing the pattern of fluid flow past shells and by calculating shell drag coefficients. Flow visualization experiments show that shell flow patterns are characterized by boundary layer separation along the flank of the outer whorl, and by turbulence in the umbilicus and behind the shell. Tow-tank measurement of drag and velocity shows that variation in shell geometry causes significant variation in drag coefficient. Inflated, depressed, and widely umbilicate shells have high drag coefficients (generally greater than 0·6–0·7). Shells that delay separation (e.g. compressed, involute oxycones) have low drag coefficients (about 0·1), but this is more than an order of magnitude greater than drag coefficients of rapid-swimming fish and squids. For most shell types change in shell orientation during swimming results in slightly higher drag coefficients as velocity increases. Analogy with aircraft and ship appendages suggests that extension of the body behind the shell has virtually no effect on drag coefficient.

FOR most animals mode of life and locomotion are so closely interwoven that the two terms are practically synonymous. Not surprisingly, locomotion has become a key issue in interpreting the mode of life of fossil ectocochliate cephalopods (ammonoids and nautiloids). Interest in the locomotion of fossil cephalopods has focused on swimming. How well did ectocochliates swim? How can the fossil record be used to evaluate swimming ability in this remarkable group of animals?

Although much has been learned about cephalopod swimming from studies relying on such palaeontological evidence as: trace fossils (Flower 1955); epizoans (Seilacher 1960, 1968; Merkt 1966; Meischner 1968; Petriconi 1971); colour patterns (Ruedemann 1921; Foerste 1930; Spath 1935); shell abnormalities (Roll 1935; Bayer 1970); shell strength (Westermann 1973); anatomical structures (Mutvei 1964; Lehmann 1971; Mutvei and Reyment 1973); and biofacies relationships (Scott 1940; Westermann 1954), information on swimming ability provided by these works is generalized or qualitative. Since swimming is a hydrodynamic process, one way to deal directly and quantitatively with the problem of cephalopod swimming ability is to analyse the hydromechanical properties of the shell. One obvious property is shell streamlining because streamlining and swimming ability are directly related to one another (Hertel 1966; Alexander 1967, 1968), and because the shell is the only ectocochliate body part commonly preserved in the fossil record.

Previous studies on shell streamlining (Schmidt 1930 and Kummel and Lloyd 1955) illustrate the practicality and informativeness of this approach. Kummel and Lloyd used a circulating water channel and balance system to determine the 'relative drag coefficients' of plaster casts of twenty species of coiled ectocochliates. Their data suggest that streamlining varies with shell form, and thus that fossil cephalopods may have displayed considerable difference in swimming ability. However, further research is needed to clarify relationships between shell form, streamlining,

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and swimming ability, and to develop a more thorough understanding of the role of streamlining in the adaptive strategy of fossil cephalopods.

This paper presents the results of experiments on patterns of flow around cephalopod shells and also measurement of drag coefficient for a wide range of shell types. The objectives were first to see how drag is produced by a shell, and secondly to determine how shell geometry, shell orientation, and body extension influence drag coefficient. Subsequent work will consider the effect of shell sculpture on drag coefficient, and examine swimming ability and the adaptive significance of shell form.

SWIMMING, STREAMLINING, AND DRAG COEFFICIENT

The velocity of any self-propelled body with a limited source of propulsive energy is a function of its hydrodynamic efficiency, i.e. the efficiency with which its thrust is converted to velocity. For aquatic animals of the size of cephalopods, hydrodynamic efficiency is determined by body morphology. Body forms that generate little drag conserve a swimmer's energy expenditures, while forms which cause much drag waste energy. The relation between these variables is given by:

$$D_F = \tfrac{1}{2}\rho V^2 A C_D \qquad \text{(Eq. 1)}$$

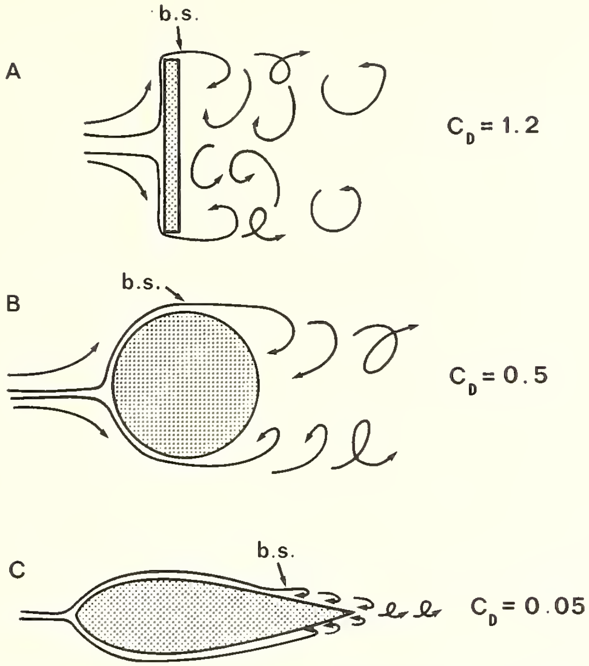
where D_F is drag force; ρ is fluid density; V is swimming velocity; A is an area representative of the animal; and C_D is the drag coefficient. A can be thought of as representing body size, and C_D as representing body shape. Since thrust equals drag when velocity is constant, C_D is an index of a body's hydrodynamic efficiency.

The magnitude of the drag coefficient is a function of the degree to which body form inhibits undisturbed flow around a swimming animal. Well streamlined animals produce minimal drag because their slender, fusiform bodies cause little flow disruption. They have small drag coefficients, and are highly efficient. Conversely, poorly streamlined animals cause much disruption, and have larger drag coefficients and low efficiencies. Streamlining and flow disruption for inanimate bodies of various shapes are diagrammed in text-fig. 1.

Streamlining and hydrodynamic efficiency are factors of considerable importance to aquatic animals. Virtually all rapid swimmers, regardless of their mode of propulsion or phylogenetic relationships, have well-streamlined, highly efficient body shapes (Hertel 1966). Conservation of locomotive energy is not so critical a need among poor swimmers, and hence such animals are invariably poorly streamlined and less efficient. The ubiquitous need for rapid swimming organisms to utilize their limited locomotive energy supply in the most economical way ensures that this correlation between body morphology and swimming ability extends to ectocochliates. We should thus be able to obtain a good idea of cephalopod swimming ability by measuring shell drag coefficients.

EXPERIMENTAL METHODS

The experimental portion of this work consists of determining drag coefficients and mapping flow patterns using instruments and procedures commonly employed in



TEXT-FIG. 1. Flow fields around three bodies of different shape in subcritical flow, i.e. Reynolds number $< 5 \times 10^5$ (Reynolds number = (body length . velocity)/kinematic viscosity). A, flat plate held perpendicular to flow; B, sphere; C, wing.

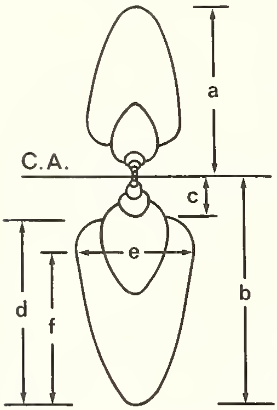
studies on applied fluid dynamics. These are: 1, measurement of drag force and velocity; and 2, flow visualization. Shell scale models were used in the experiments instead of actual shells because the models are morphologically less complex, and as a result more easily analysed.

Scale models of cephalopod shells. Thirty-four plexiglas shell models were constructed following the technique previously described (Chamberlain 1969). Morphological differences between the models are restricted to variation in two shell parameters. Other shell characteristics, although commonly variable among real shells, are held constant in the models. The form of each model adheres to the logarithmic paradigm; ontogenetic variation in shell shape does not occur. The morphological variables are:

1. Whorl expansion rate (*W*)—roughly equivalent to whorl inflation;
2. Distance of the whorls to the coiling axis (*D*)—roughly equivalent to the size of the umbilicus.

W and *D* are two of the four parameters used by Raup (Raup 1961, 1962, 1966; Raup and Michelson 1965) in describing basic geometry of coiled shells, and are defined in text-fig. 2. All models have a unique combination of W and D, but are identical to one another in other respects. The morphological constants are:

1. Relative whorl thickness (S)—models have circular whorl sections ($S=1$); whorl height = whorl width;
2. Translation rate (T)—all models are planispiral ($T=0$);
3. Flank position (F)—all models have their greatest whorl width at the mid-point of whorl height;
4. Surface relief—all models are smooth surfaced, none have ribs, spines, or aperture adornments;
5. Size—all models have maximum diameters of 12·7 cm.



TEXT-FIG. 2. Definition of geometric parameters of shell form. $W=(b/a)^2$; $D=(b-d/b)$; $S=(e/d)$; $F=f/(b+a)$.

S, T, and F are defined in text-fig. 2. S and T are the other two geometric parameters of Raup, and along with W and D are discussed more fully in his previously cited papers. It should be stressed that since the form of each model is defined parametrically all models have strictly hypothetical morphologies. None are patterned after real prototypes, although many closely approximate shells of actual species. Table 1 gives values of W, D, S, and F for each specimen used in this experiment.

Two models (35 and 36 in Table 1) have compressed whorl sections ($S < 1$), and hence closely resemble the discoid form of oxycones. Otherwise they are identical to the thirty-four models used in the main experiment. In addition, drag and velocity measurements were made for the shell of an adult *Nautilus pompilius*. Although this treatment of variation in whorl shape obviously deals with only a token sample of the total range in this variable, it should indicate the magnitude of streamlining differences to be expected between compressed and depressed shells. Results of a more detailed analysis of the effect of whorl shape on drag coefficient will be presented in due course.

Drag and velocity measurement. It is clear from equation 1, that drag coefficient may be calculated from known values of D_F, V, ρ, and A. The density of water is known, and the representative area can be determined from the equations of Raup and Chamberlain (1967) for shell volume (shell volume raised to the 2–3 power is used as a representative area), or by water displacement. Only drag force and velocity need be determined experimentally.

To measure these two parameters, the tow tank at the Ship Hydromechanics Laboratory of the United States Naval Academy was used. A remote-controlled carriage is fitted to an overhead monorail and lateral drive rail, and moves along the length of the tank at velocities up to about 10 m/sec. Objects to be tested are suspended from the carriage, and dragged through the water. Drag force is measured by an electronic device which records distortion in the carriage frame resulting from drag on the towed object. A photocell system mounted at one end of the tank measures carriage velocity which is pre-set. Drag and velocity are continuously monitored throughout the run, and the data digitized and recorded electronically. Thirty to

TABLE 1. Geometric parameters and drag coefficients of specimens studied. All are models, except 37 which is a *Nautilus* shell.

Specimen (model number)	Shell geometry				C_D in 30° Att.	Calc. rest Att.	C_D in rest Att.	Other Att.	C_D in other Att.
	W	D	S	F					
1	1·5	0·1	1·0	0·25	0·39	120	0·37		
2	2·0	0·1	1·0	0·26	0·52	63	0·48		
3	2·5	0·1	1·0	0·28	0·57	38	0·48		
4	3·0	0·1	1·0	0·29	0·66	24	0·58		
5	3·5	0·1	1·0	0·29	0·63	16	0·75		
6	4·0	0·1	1·0	0·30	0·64	10	0·77		
7	4·5	0·1	1·0	0·31	0·67	5	0·85		
8	5·0	0·1	1·0	0·31	0·69	1	0·95		
9	1·5	0·2	1·0	0·22	0·54	122	0·51		
10	2·0	0·2	1·0	0·23	0·57	65	0·49		
11	2·5	0·2	1·0	0·25	0·52	40	0·46		
12	3·0	0·2	1·0	0·25	0·73	26	0·65		
13	3·5	0·2	1·0	0·26	0·70	17	0·66		
14	4·0	0·2	1·0	0·27	0·63	10	0·64	90	0·49
15	4·5	0·2	1·0	0·27	0·75	5	0·82		
16	5·0	0·2	1·0	0·27	0·72	2	0·80		
17	1·5	0·3	1·0	0·19	0·46	124	0·48	90	0·44
18	2·0	0·3	1·0	0·20	0·51	67	0·48		
19	2·5	0·3	1·0	0·21	0·58	41	0·51		
20	3·0	0·31	1·0	0·22	0·59	25	0·56		
21	3·5	0·3	1·0	0·23	0·71	16	0·67		
22	4·0	0·3	1·0	0·23	0·66	10	0·72		
23	4·5	0·3	1·0	0·24	0·70	6	0·78		
24	5·0	0·3	1·0	0·24	0·73	2	0·85		
25	1·5	0·4	1·0	0·17	0·51	121	0·49		
26	2·0	0·43	1·0	0·17	0·44	67	0·44		
27	2·5	0·4	1·0	0·18	0·56	38	0·49		
28	3·0	0·4	1·0	0·19	0·67	25	0·63	10	0·67
29	4·0	0·4	1·0	0·20	0·92	10	0·81		
30	1·5	0·5	1·0	0·14	0·49	111	0·51		
31	2·0	0·5	1·0	0·15	0·50	61	0·45		
32	2·5	0·5	1·0	0·15	0·67	38	0·58		
33	3·5	0·5	1·0	0·16	1·10	16	1·15		
34	1·5	0·6	1·0	0·11	0·55	115	0·49		
35	2·0	0·2	0·5	0·27	0·32				
36	2·0	0·5	0·3	0·35	0·25				
37	3·25	0·05	0·7	0·51	0·48				

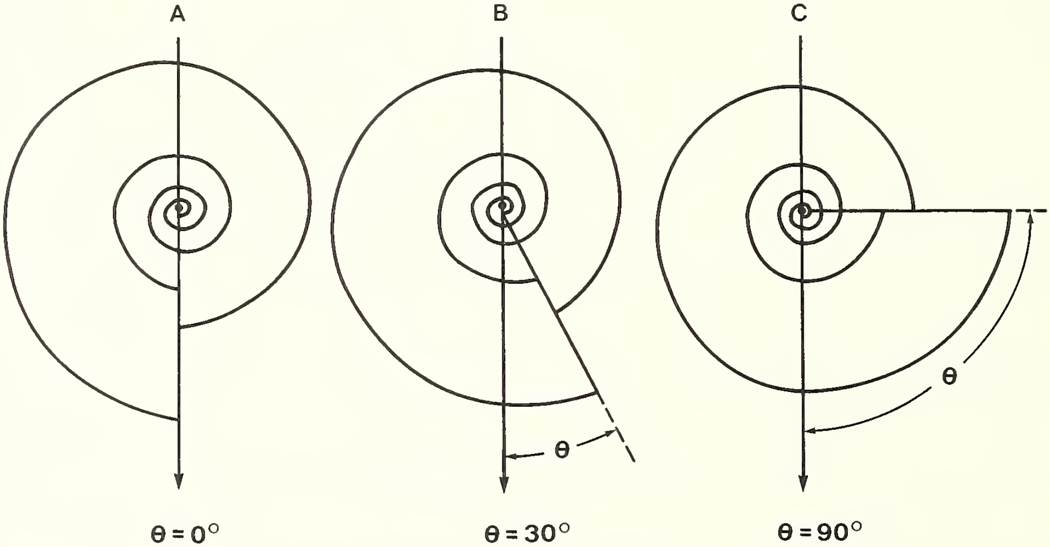
forty separate drag determinations were made for each model at velocity intervals from about 10 cm/sec to about 250 cm/sec.

Flow visualization. Visualizing flow around an animal is important because it can indicate how drag is produced, and how change in morphology alters drag coefficient. Flow visualization has proved valuable in relating shell form to feeding habits in brachiopods (Rudwick 1961; Wallace and Ager 1966; Shiells 1968; Savage 1972), bivalves (Stanley 1970), and reef corals (Kawaguti 1943; Chamberlain and Graus 1972, 1975).

Small crystals of potassium permanganate were cemented to the venters and other critical areas of the specimens with latex glue. The crystals dissolve, releasing streams of violet dye whose downstream movements trace the pattern of flow around the specimen. Another series of tests using methylene blue and amido black dyes was done in order to observe boundary layer flow more clearly. Dye was injected from an overhead reservoir into the boundary layer at the venter of each model tested. The epoxy surface of the model was stained blue where the boundary layer is attached to the surface of the model, but remains uncoloured where the boundary layer has separated. These experiments were carried out with the low turbulence flume located in the Department of Mechanical Engineering, McMaster University.

Experimental constraints. The models were placed in lifelike positions during testing in order to simulate cephalopod swimming behaviour. All tests were done with the specimens orientated with their apertures directed posteriorly relative to water movement. The results reported here thus apply to the peculiar cephalopod habit of swimming backwards.

Wings and plates have widely differing lift and drag properties, depending on their angle of attack (Prandtl and Tietjens 1934; Hoerner 1965). The possibility of such behaviour occurring in cephalopods requires standardization of the 'swimming attitude' of the models. Thus one series of tow-tank tests was conducted in which the models were orientated with the aperture turned down and inclined about 30° to the vertical. This attitude was selected because it corresponds to the attitude of *Nautilus* when at rest (see text-fig. 3). Trueman (1941) and Raup (1967) have demonstrated that attitude depends upon the length of the body chamber so that the normal rest attitude of many species was probably different than that of *Nautilus*. Thus, a second series of tests was made in which the models were oriented as shown in



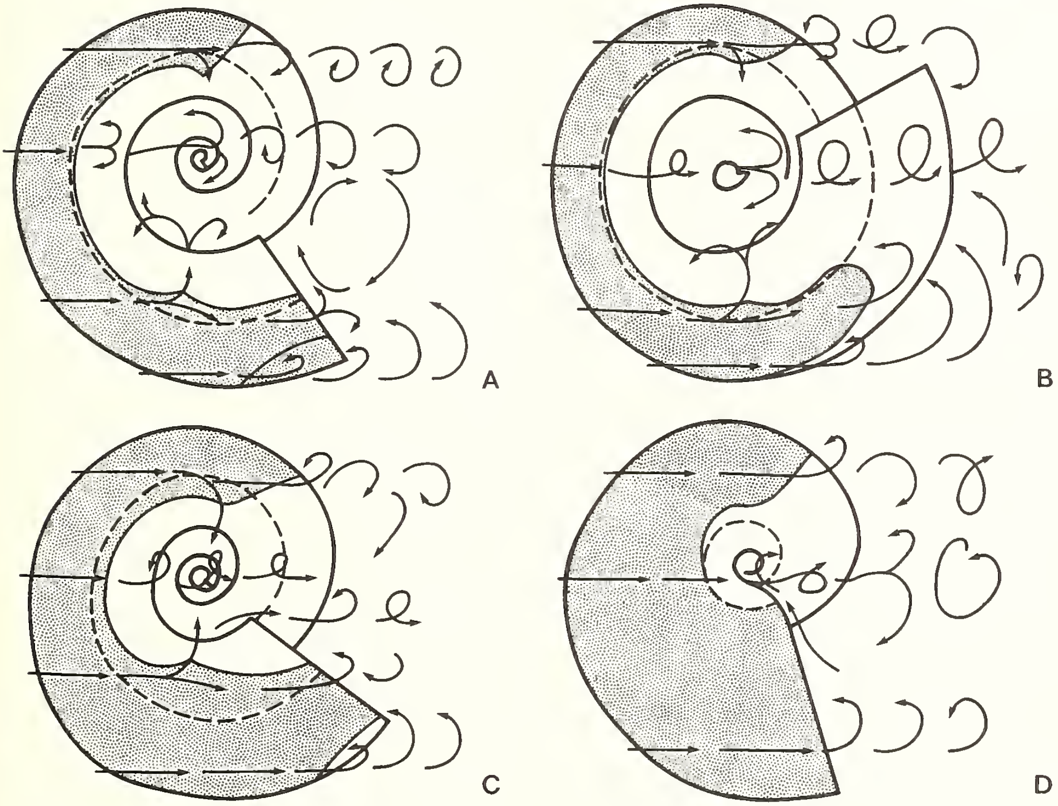
TEXT-FIG. 3. Orientation of the shell is defined as the angle (θ) between the aperture and the vertical (heavy downward arrow). A, $\theta = 0°$; B, $\theta = 30°$; C, $\theta = 90°$.

Table 1, column 7. These attitudes were calculated from the equations of Raup and Chamberlain (1967), and represent probable rest attitudes of animals having shells identical in external morphology to the models. Bidder (1962) reported that *Nautilus* 'rocks' (i.e. rotates in the vertical plane) during swimming. As both Trueman and Raup have noted, fossil ectocochliates may have behaved similarly. The effect of rocking was studied by testing three models representing widely different morphologies in orientations not covered in either of the two main series of tests (see Table 1, column 9).

SHELL FLOW PATTERNS

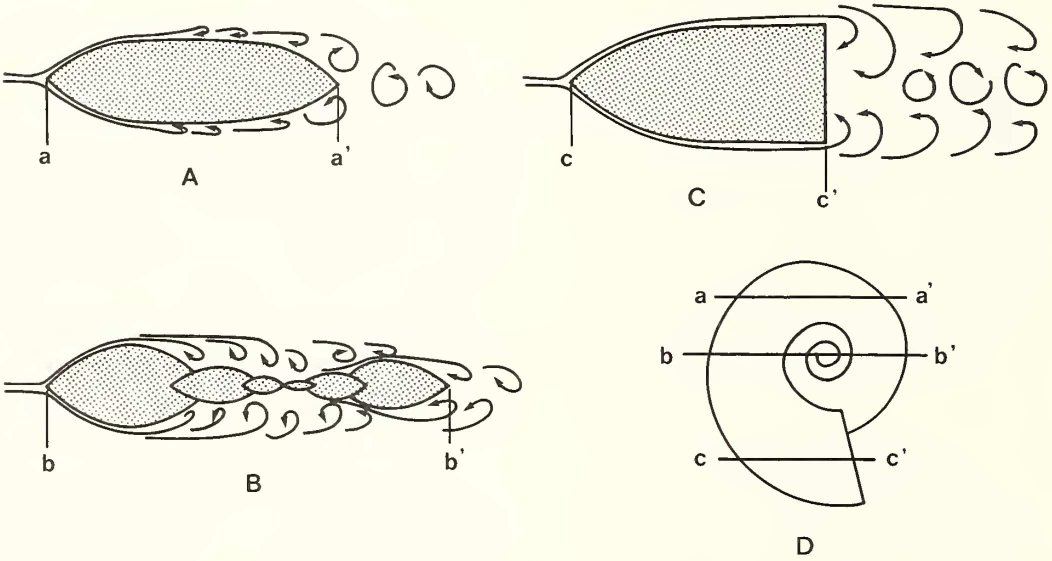
Drag is produced by discontinuities in the speed and direction of water moving past a body. As shown in text-fig. 1, drag depends on such major discontinuities as flow separation and wake turbulence. The manner in which shell form controls separation and turbulence is best understood by analysing shell flow patterns.

Passage of water around a cephalopod shell is shown in Plate 84 and text-fig. 4.



TEXT-FIG. 4. Sketch of flow lines shown in Plate 84. A, lytoceratid shell model (no. 26); B, serpenticonic shell model (no. 9); C, widely umbilicate oxyconic shell model (no. 35); D, *Nautilus pompilius* (no. 37). Area of boundary layer attachment shown by stippling. Dashed line marks umbilical shoulder on outer whorl.

The basic flow pattern illustrated here occurs with only minor modification for all specimens tested, and for all planispiral shells. Water passes smoothly across the venter and anterior part of the leading whorl, but in doing so loses momentum. As it approaches the umbilical shoulder, the flow stalls and then separates from the surface of the shell. These two events are shown in Plate 84 as a concentration of dye and distortion of the dye streams along the flank of the leading whorl. Flow is attached only to the leading part of the shell. The umbilicus and posterior portion of the shell are immersed in relatively stagnant water. Separation on the forward part of the shell creates a well-developed turbulent wake, shown in Plate 84 by swirls of dye behind the shell and in the umbilicus. Water movements near the surface of the shell are detailed in text-fig. 5. For the most part, post-separation flow at the surface consists of small, unstable vortices. Suction created behind the shell and extending into the umbilicus is sufficiently strong, however, to set up a weak, relatively stable vortex which in many shells brings water up from the wake into the umbilicus (Pl. 84, fig. 4). In addition, some water is diverted directly into the umbilicus from the flow on the outer whorl (Pl. 84, fig. 3). Thus, the major characteristics of



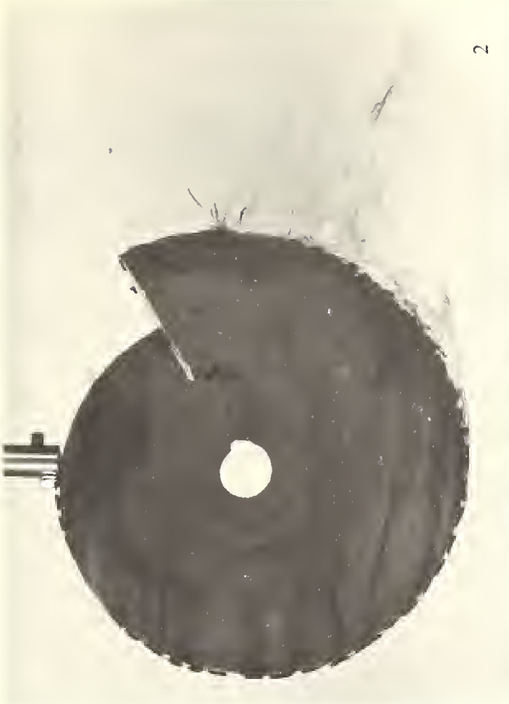
TEXT-FIG. 5. Cross-sections through flow field of model no. 35, showing details of water movement near surface of shell. A, top of shell; B, through umbilicus; C, bottom of shell and aperture; D, lateral view of shell showing position of cross-sections.

EXPLANATION OF PLATE 84

Flow fields of four specimens in rest orientation. Lines of flow made visible by violet dye bleeding from crystals of potassium permanganate cemented to venter. All ×0·25.

Fig. 1. Lytoceratid shell model (no. 26).
Fig. 2. Serpenticonic shell model (no. 9).
Fig. 3. Widely umbilicate oxycone shell model (no. 35).
Fig. 4. *Nautilus pompilius* (no. 37).

PLATE 84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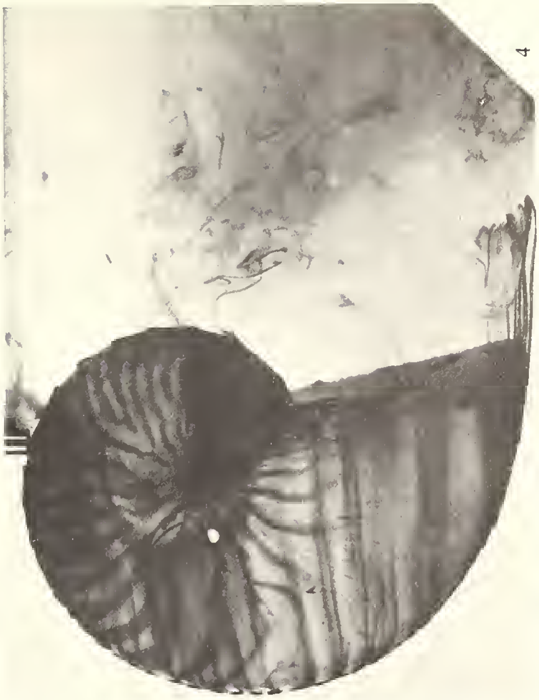
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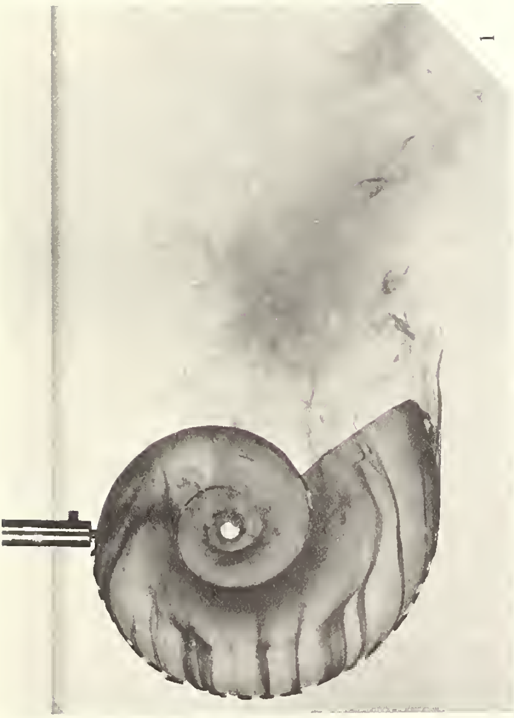
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3

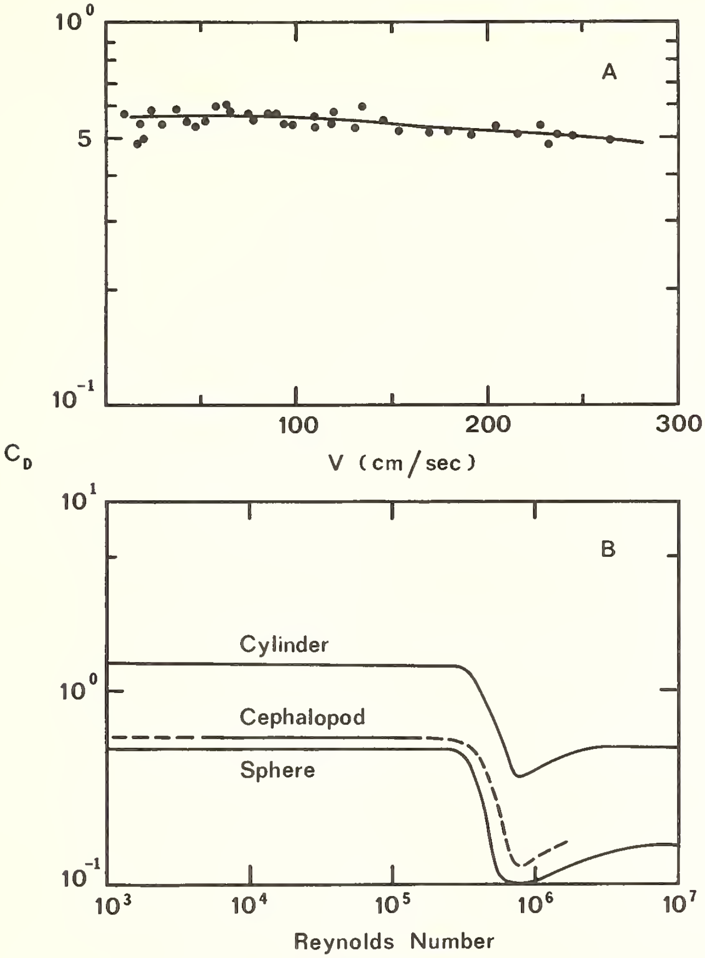
CHAMBERLAIN, Flow fields of cephalopods

flow around a cephalopod shell are separation along the flank, a turbulent wake behind the flank of the leading whorl, and a turbulent umbilicus.

Shell morphology controls the structure of the flow in a number of ways. First, the position of flow separation is influenced by the curvature of the shell surface. A smooth, gently curving shell retards momentum loss in the boundary layer, and permits the flow to remain attached over more of the surface. The size of the umbilicus also influences separation. Since the flow separates at the umbilical shoulder, shells having the umbilical shoulder displaced toward the coiling axis will allow the flow to remain attached over more of the shell surface (compare Pl. 84, fig. 1, and text-fig. 4A, with Pl. 84, fig. 4, and text-fig. 4D). Shell compression is important because compressed shells invariably have more gently curving surfaces than do wider, more robust shells. Moreover, compressed shells have relatively small frontal areas (projected area in direction of flow), and therefore intercept and redirect less water per unit of shell volume. The result is smaller wakes and less flow perturbation. Finally, the absence of a solid surface behind the aperture can force premature separation over this part of the shell (Pl. 84, figs. 3 and 4; text-fig. 4C, D). The magnitude of this effect should depend on the size of the aperture relative to the size of the shell. Thus, four aspects of shell form appear to be important in structuring the flow—curvature of the shell surface, relative size of the umbilicus, degree of shell compression, and relative size of the aperture. No one factor appears to play a pre-eminent role in generating drag over the entire range of shell form studied, but in specific instances components of one or two may predominate.

DRAG COEFFICIENT AND VELOCITY

Although Schmidt did not record the effect of velocity on the drag coefficients of his four specimens, Kummel and Lloyd observed that their 'relative drag coefficient' appeared in most cases to have some dependence on velocity. However, the results of the present work suggest that shell drag coefficients are virtually constant over the velocity range studied. From text-fig. 6A, which shows a typical plot of drag coefficient versus velocity, drag coefficient can be seen to diminish only slightly as velocity increases. The other models show this same near constancy in drag coefficient. In this respect, cephalopod drag coefficients compare favourably with drag coefficients of other bodies under similar flow conditions (see text-fig. 6B). This observation should not be construed as indicating that cephalopod drag coefficients are always constant, however, since drag coefficients do change when flow conditions change. In text-fig. 6B, for example, the abrupt decrease in drag coefficient at Reynolds numbers (Re) of about 5×10^5 marks the transition between laminar and turbulent boundary layer flow. It is of interest to note that although produced by a change in flow state, this decrease can be affected by body morphology, and represents an event of considerable importance to swimmers. Drag coefficient changes of this magnitude do not appear in the present data because Reynolds numbers for this work ($5{\cdot}2 \times 10^3 \leqslant \mathrm{Re} \leqslant 1{\cdot}8 \times 10^5$) are less than the critical value of 5×10^5, as illustrated in text-fig. 6B. At supercritical Reynolds numbers (i.e. above 5×10^5), shell drag coefficients can be expected to be lower than reported here, as sketched by the dashed line in text-fig. 6B.



TEXT-FIG. 6. Drag coefficient of shell model 9. A, C_D versus velocity (V). Each dot represents one constant-velocity tow-tank run. B, comparison of C_D for model 9 with C_D of sphere and cylinder as a function of Reynolds number.

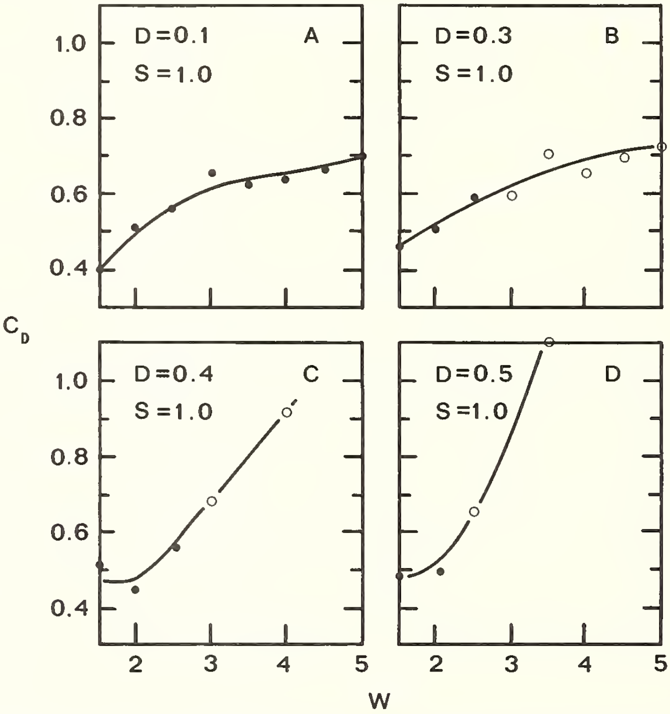
Since model drag coefficients are virtually constant over the entire velocity range examined here, an average drag coefficient for each model was calculated by straightforward numerical means. Average drag coefficients for all specimens are given in Table 1, and as for model 9 in text-fig. 6, apply only for laminar boundary flow (i.e. Re $< 5 \times 10^5$).

DRAG COEFFICIENT AND SHELL GEOMETRY

The basic geometrical parameters, W, D, S, and F, control flow structure by controlling shell form. Since several factors are thus involved, drag can be expected to result from a complex interaction of morphologic components. The role of any one parameter (say W) can be determined from tow-tank data from a suite of models in which the other three parameters (S, D, and F), and orientation are constant. The role of each of the other parameters can be obtained similarly.

Whorl expansion rate (W). Text-fig. 7, shows plots of C_D against W. For each plot S, D, and orientation (= 30°) are constant, and variation in F is negligible. Inspection of these graphs shows that: (1) C_D varies directly with W; and (2) whorl offlap increases the rate of change of C_D with W. Thus, in shells with roughly circular whorl sections high W morphologies are generally more poorly streamlined and less efficient than low W shells.

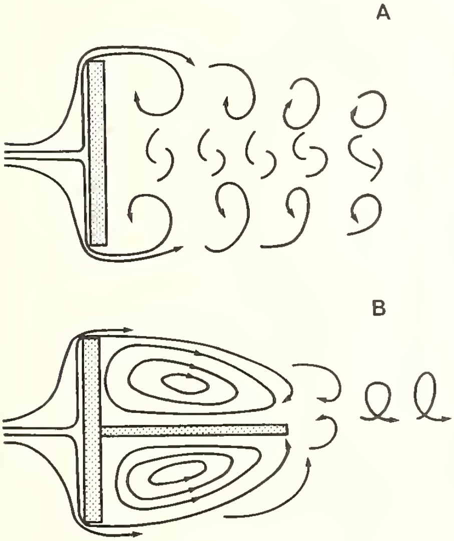
The explanation for this relationship lies in the kind of morphological changes that result from variation in W, and in the effect of these changes on flow structure. Increase in W produces progressively greater degrees of shell inflation. Inflated shells are wider relative to their size than their deflated counterparts, and as a consequence intercept and divert a relatively larger column of water. The result is more drag and higher drag coefficients in the high W end of the morphological spectrum. Although the aperture becomes a significant morphologic feature at high W, its importance in generating drag in $S = 1$ shells is probably secondary, at least when orientation is 30°. As shown in Plate 84, most of the flow separates before it actually reaches the aperture. The aperture operates in the wake of the umbilicus and anterior



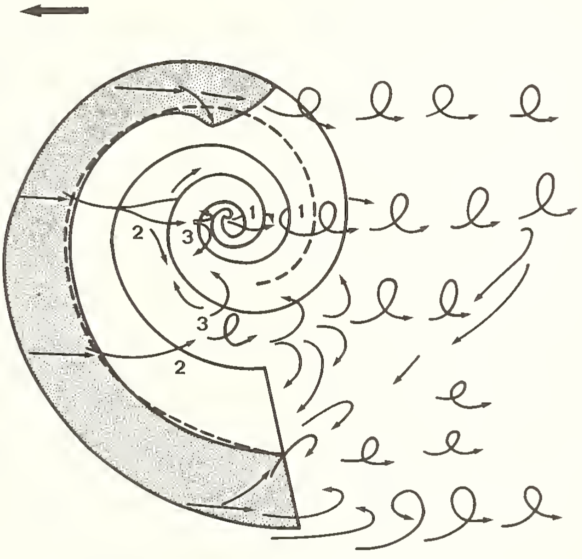
TEXT-FIG. 7. Drag coefficient (C_D) versus expansion rate (W). Dots—shells with whorl overlap. Circles—shells with whorl offlap. A, $D = 0{\cdot}1$, $S = 1{\cdot}0$; B, $D = 0{\cdot}3$, $S = 1{\cdot}0$; C, $D = 0{\cdot}4$, $S = 1{\cdot}0$; D, $D = 0{\cdot}5$, $S = 1{\cdot}0$.

part of the shell, and hence exerts relatively little influence on flow separation. As a result, the contribution of the aperture to total shell drag is probably correspondingly small.

The marked increase in drag coefficient associated with complete whorl exposure (text-fig. 7C, D) is probably brought about in two ways. The first, which could be called the 'splitter-plate' effect, derives from the influence of the shell on wake turbulence. Ordinarily, the wake consists of a fairly ordered array of vortices. When a flat plate (splitter plate) or similar object is appended to the rear of a body and aligned parallel to its direction of motion, it effectively restricts circulation in the wake and reduces vortex size (see text-fig. 8). The result is less drag. In cephalopod shells, most of the flow separates on the anterior flank, so that the umbilical and posterior regions of the shell actually operate inside the wake (Pl. 84, text-fig. 5). When the whorls overlap the trailing part of the shell acts as a splitter plate by limiting the scale of fluid movement near the shell. Whorl exposure diminishes the splitter-plate effect of the shell by permitting water to be drawn into oscillatory movements through the open spaces between successive whorls (text-fig. 9). Turbulence is enhanced and drag coefficient increases.

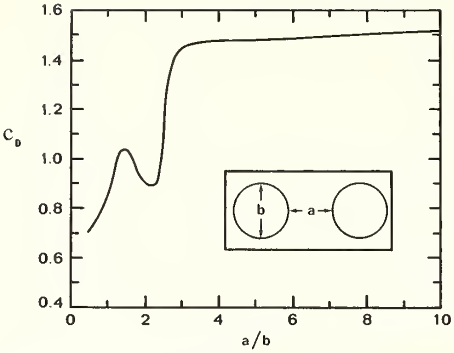


TEXT-FIG. 8. Effect of splitter plate on vortex structure in wake of perpendicular flat plate. Redrawn from fig. 3-1 of Hoerner 1965. A, perpendicular flat plate; B, perpendicular flat plate + splitter plate.



TEXT-FIG. 9. Flow pattern around a gyrocone (model no. 33). Water moves through openings between whorls. 1, flow diverts around posterior whorls. 2, flow diverts into umbilicus. 3, backflow into umbilicus.

The second way in which offlap affects the flow is by increasing the drag of the inner whorls. When whorls overlap, the inner whorls are shielded by the anterior portion of the outer whorl, and as a result should not in themselves generate much drag. Offlap reduces this 'shield effect' by exposing inner whorls to the flow. The situation is analagous to that diagrammed in text-fig. 10, for two identical cylinders arranged in tandem. As the distance between the two cylinders increases, the posterior cylinder acquires its own wake. The total drag on the two-cylinder system increases with increasing inter-cylinder distance, and reaches a maximum when the two cylinders are sufficiently distant to allow the wake elicited by the first one to subside before the passage of the second. Whorl separation never reaches the magnitudes diagrammed for cylinders, but flow visualization shows that in many gyrocones inner whorls are sufficiently distant from the leading edge of the shell, and from one another, to create their own weak wakes, and thus add to the drag of the whole shell (see text-fig. 9).

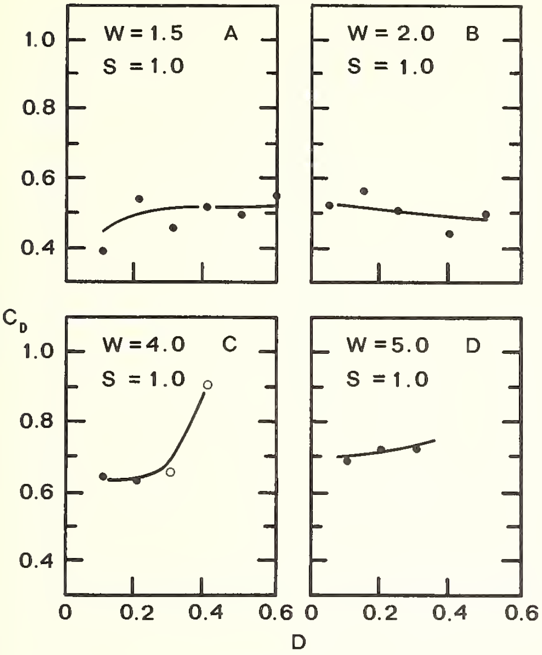


TEXT-FIG. 10. Drag coefficient of tandem cylinders as a function of distance between cylinders; C_D based on frontal area of forward cylinder. Data from Hoerner 1965. Inset shows definition of parameters: *a*—distance between cylinders; *b*—cylinder diameter.

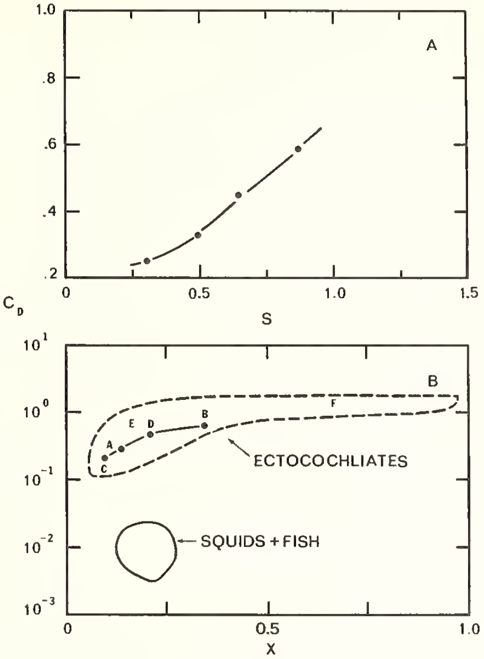
Distance to the coiling axis (D). Text-fig. 11 shows how C_D varies with D. At low $W (1\cdot5 \leqslant W \leqslant 3\cdot0)$ the magnitude of change in C_D is relatively small as long as the whorls are overlapped. For $W > 3\cdot0$, C_D increases with D, especially when offlap becomes pronounced. These observations can be interpreted in terms of variation in the size of the umbilicus. Umbilical dimensions increase from low to high D. The small umbilicus characteristic of low D, involute, shells permits the flow to remain attached to a greater portion of the shell's surface (as in Pl. 84, fig. 4; and text-fig. 5D). Separation is delayed, the umbilical drag component lessened. In contrast, high D, evolute, shells have broad umbilici and umbilical shoulders placed further forward on the shell. As in the case of the lytoceratid model illustrated in Plate 84, fig. 1, and text-fig. 5A, most of the flow is forced to separate near the leading edge of the shell. Only a small portion of the flow remains attached to posterior surfaces. The result is a gain in the umbilical drag component as D increases. Note that the position of separation on the shell depends on the size of the umbilicus, not on its morphology. The physical characteristics of the umbilicus—its depth and surface features—can be expected to exert little influence on drag.

D-related changes in shell compression and relative aperture size act in opposition to the effect of the umbilicus. Increased D results in relatively narrower shells having relatively smaller apertures (see Raup 1967). Thus, as D increases the drag components due to these two factors are reduced. Undoubtedly this inverse relationship partially offsets the effect of umbilical size, and results in the small slope in the onlap region of the $C_D - D$ plots in text-fig. 11.

Whorl shape (S *and* F). The effect on drag coefficient of variation in S can be estimated by using drag data for specimens with $S \neq 1$. Text-fig. 12A shows this data. The specimens upon which this figure is based incorporate some variation in W, D, and F, so that the curve shown in text-fig. 12A indicates only the general trend in drag coefficient as a function of S. Nevertheless, it is evident that variation in S can produce a significant decrease in shell drag coefficient. The direct relation



TEXT-FIG. 11



TEXT-FIG. 12

TEXT-FIG. 11. Drag coefficient (C_D) versus distance to coiling axis (D). Dots—shells with whorl overlap. Circles—shells with whorl offlap. A, $W = 1{\cdot}5$, $S = 1{\cdot}0$; B, $W = 2{\cdot}0$, $S = 1{\cdot}0$; C, $W = 4{\cdot}0$, $S = 1{\cdot}0$; D, $W = 5{\cdot}0$, $S = 1{\cdot}0$.

TEXT-FIG. 12. Drag coefficient (C_D) versus shell compression. A, data from specimens, plotted as a function of whorl shape; B, comparison of estimated ectocochliate drag coefficients with those of rapid-swimming fish and squids. X, fineness ratio. For fish and squids, X = body width/body length. For ectocochliates, X = maximum shell width/maximum shell diameter. Ectocochliate region shows approximate range in shell drag coefficient as a function of W, D, and F. Curve same as in A. Letters within ectocochliate region represent: A—evolute oxycones; B—gyrocones; C—involute oxycones; D—nautilicones; E—serpenticones; F—cadicones. Data for fish primarily from Magnan (1930) and Hertel (1966). Drag coefficients for squid estimated from performance data on *Loligo* (Trueman and Packard 1968; Packard 1969) and *Dosidicus* (Cole and Gilbert 1970).

between S and C_D can be explained in terms of shell compression. As whorls become more compressed (S decreases, F constant), the surface of the leading portion of the shell becomes more gently inclined. This diminishes the rate of momentum loss in the boundary layer, and permits the flow to remain attached for some distance into the interior of the umbilicus (Pl. 84, fig. 3; text-fig. 5C). In addition, whorl compression produces less flow disturbance as explained above. Displacement of the umbilical shoulder toward the coiling axis (S constant, F increases) may account for some of the variation in text-fig. 12A because the low S specimens in this figure (model 36 and *Nautilus*) also have high F.

The estimated effect of variation in W, D, and F at various values of S is shown in text-fig. 12B. At $S = 1$, variation in these parameters leads to a range in C_D of about 0·4–1·1, with values greater than about 0·75 being restricted to gyrocones (text-figs. 7 and 11). Shells with higher S (whorl width > whorl height) develop a pronounced bluntness of the leading edge. High drag coefficients, which accompany bodies of such bluntness, offset any gains possibly deriving from variation in *W*, *D*, or *F*. The lower limit of high *S* (cadiconic) shells should thus be higher than when $S = 1$, as shown in text-fig. 12B. As in $S = 1$ shells, this lower limit should be found in shells with low to medium $W (1{\cdot}5 \leqslant W \leqslant 3{\cdot}0$, approximately) and low $D (0{\cdot}1 \leqslant D)$. High *F* would also favour lower drag coefficient in these shells. Among high *S* shells, gyrocones should have the highest drag coefficients for the same reasons as discussed above, but they should not differ greatly in this respect from $S = 1$ gyrocones. Drag coefficients as large as those of gyrocones ($C_D \geqslant 1{\cdot}0$) are not appreciably influenced by changes in body shape (for a two-dimensional circular cylinder ($S = 1$), $C_D = 1{\cdot}1$; for a perpendicular flat plate ($S = \infty$), $C_D = 1{\cdot}2$). The range in drag coefficient for high *S* shells thus should be about $0{\cdot}6 \leqslant C_D \leqslant 1{\cdot}2$.

At low *S* (whorl height > whorl width) drag coefficients should be correspondingly low as explained above. But within a suite of low *S* shells, drag coefficient will still be a function of *W*, *D*, and *F*, and will vary as described above for robust shells, i.e. lower drag coefficients will occur when *W* and *D* are low, and *F* high. In fact, the lowest shell drag coefficients, and hence most efficient of all coiled shell types, should be found among low *S* shells ($S \leqslant 0{\cdot}25$) having very low *D* ($D \leqslant 0{\cdot}25$) and high *F* ($F \approx 0{\cdot}4$–$0{\cdot}5$), i.e. involute, high-shouldered oxycones. However, it is unlikely that ectocochliate drag coefficients approach those of well-streamlined objects like wings and hydrofoils, or the bodies of rapid-swimming fish and squids, because the overall form of cephalopod shells differs from the fusiform streamlining paradigm exemplified by these other bodies by retaining two morphological irregularities—the umbilicus and aperture. Relatively little drag should be produced by separation at the umbilicus or aperture, since these features are reduced in involute oxycones. But when drag coefficient is already low, as it is in these shells (text-fig. 12A), even small drag additions significantly increase drag coefficient. The extent of umbilical and aperture separation shown in Plate 84, figs. 3 and 4, suggest that a drag coefficient of about 0·1 at $\mathrm{Re} \approx 10^4$ is a reasonable estimate for high-shouldered, involute oxycones. Thus, the best streamlined cephalopod shells are probably more than an order of magnitude more poorly streamlined and inefficient than the bodies of modern swimmers (text-fig. 12B). For equal expenditures of propulsive energy, a fusiform fish, for example, could probably travel at least ten times faster and ten times further than an ectocochliate of equal size.

Since the low drag coefficients of involute oxycones depend to a great extent on very small umbilici, it can be expected that umbilical size will have a much greater influence on drag coefficient in compressed shells than in robust ones. As *D* increases from 0·05, for example, drag coefficient should rise markedly as the umbilicus widen rather than slowly as when $S = 1$. Since whorl exposure produces a large amount of turbulence regardless of whorl shape, comparatively high drag coefficients should be found among low *S* gyrocones. However, analogy with tandem streamlined struts (which generate less drag than a similar arrangement of cylinders, Hoerner 1965), suggests that such shells probably do not attain the high C_D values of high *S* gyrocones, and may not exceed $C_D \approx 0{\cdot}8$.

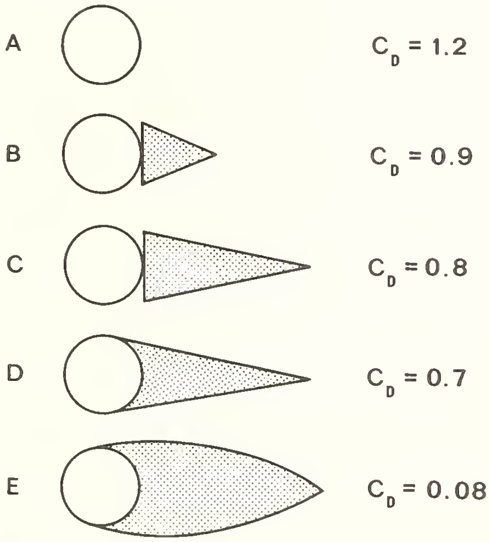
DRAG COEFFICIENT AND BODY EXPOSURE

In modern *Nautilus* the tentacles and portions of the head can be extended outward from the aperture (Bidder 1962; Stenzel 1964; Denton and Gilpin-Brown 1966). Some evidence has been developed which suggests a similar ability in fossil ectocochliates (Flower 1955, on tentacular trace fossils; Crick 1898; Mutvei 1957, 1964; Sweet 1959; Jordan 1968, on muscle scars), and it is generally believed that most fossil forms were capable of such movement. Since any exposed surface can interact with the flow, the extension of the body behind the shell could conceivably alter drag coefficient.

In squids the head and arms continue the gentle curvature of the rest of the body, and impart a well-streamlined, fusiform body shape well adapted for efficient swimming. Presumably, the extended head and arms of fossil forms would act similarly, but to do so the exposed body must conform to two morphological requirements. First, the trailing mass of arms should approximate to a tapering fusiform shape as in squids. Secondly, the dimensions of the exposed body must be in accord with the dimensions of the shell. If the extended body is too small, it cannot fill the dead-water region behind the shell, or provide a gently curving surface to which the boundary layer can adhere. If it is too large, it will exceed the flanks of the shell, and cause more flow disturbance and drag than if it were not present at all.

Bidder (1962) and Denton and Gilpin-Brown (1966) observed that *Nautilus* holds its arms in a tapering mass, and Stürmer's recent X-ray studies (Stürmer 1970) indicates that the necessary arm arrangement may have been possible in some Devonian goniatites. Although *Nautilus* has a tendency to withdraw its arms during swimming (Bidder 1962), positioning of the arms in the proper way probably posed no great feat for most ectocochliates.

The effect of the size of the exposed body can be estimated by determining the extension required to significantly alter drag coefficient. This can be done by referring to data on aircraft and ship appendages. Text-fig. 13 presents data on fairings and circular cylinders used in experiments on drag reduction of aircraft gun barrels. It is apparent that substantial saving of energy (about 40% total barrel drag) can be obtained by placing tapered fairings behind the barrels. But it is also apparent that in order to be of service the fairings must be about as large as the barrels themselves. In particular, fairing length and width should at least equal the diameter of the barrel.



TEXT-FIG. 13. Effect of tapered fairings on subcritical drag coefficients of aircraft gun barrels. Redrawn from figs. 13-50 and 13-51 of Hoerner 1965. A, barrel cross-section; B, C, D, barrel + tapered fairings of various sizes (in cross-section); E, barrel + streamlined sleeve.

Shells are not gun barrels, nor are body parts fairings, but the analogy is a useful one because it tells us that exposed parts of the body must be approximately the same size as the shell itself to obtain a significant reduction in drag coefficient. Lesser degrees of extension will result in only small or insignificant gains in energy economy because the afterbody is not large enough to give a fully developed fusiform shape to the shell-animal combination. In addition, the extended parts must cover the entire rear of the shell, not just the aperture, and should extend into the umbilicus to ensure a smooth, continuous afterbody profile. Otherwise, gaps and surface discontinuities left between the shell and body create obstacles that cause flow separation, and thereby minimize any beneficial effect body extension may have. The body of *Nautilus* is far too small to meet these criteria, even when fully extended. It would appear that *Nautilus* cannot derive much advantage from this effect.

Although our knowledge of the anatomy of fossil ectocochliates is fragmentary at best, there is ample evidence which shows that the afterbody in fossil forms also was not large enough to fully exploit this mode of drag reduction. For example, the presence of colour markings (Ruedemann 1921; Schindewolf 1928; Foerste 1930; Spath 1935) and pre-mortal epizoans (Dunbar 1928; Lange 1932; Schindewolf 1934; Seilacher 1960; Merkt 1966; and Meischner 1968) shows that shell surfaces which should have been covered by such a ponderous afterbody were actually free of even a temporary covering of flesh. Moreover, the excellent reconstructions of ectocochliate anatomy given by Mutvei (1957, 1964), Jordan (1968), and Lehmann (1971, 1972), and such rare anatomical insights as those of Flower (1955), Müller (1969), and Wetzel (1969) indicate that the fossil animal was probably fairly similar to modern *Nautilus* both in general anatomy and in the relation of the animal to its shell. We can conclude that, in general, body extension probably plays little part in altering drag coefficient in either fossil or modern ectocochliates. The statements of Schmidt (1930) that the soft parts are hydrodynamically more meaningful than many variations of the shell, or of Geczy (1960) that because of body extension shell drag does not express the drag of the whole animal, are clearly excessive.

High-shouldered, involute oxycones may be an exception to this general rule, but only if body extension were sufficient to provide a fully developed afterbody behind the aperture. In other shells, the effectiveness of such an afterbody behind the aperture would be small because the resultant drag loss would be overwhelmed by turbulence generated by other sources (e.g. umbilicus, blunt leading edge, spines, etc.). In high-shouldered, involute oxycones turbulence due to these other sources is minimal so that a considerable percentage of the total turbulence may be eliminated by body extension, and the resulting gain in energy economy may be substantial. In contrast, the poorly streamlined gyroconic form of Stürmer's goniatites suggest that these animals could not profit hydrodynamically from extension of their bodies, although the degree of extension indicated in Stürmer's radiograph is certainly sufficient to form a complete afterbody behind the aperture.

DRAG COEFFICIENT AND SHELL ORIENTATION

As in any body which is not perfectly symmetrical in three dimensions, drag elicited by a cephalopod shell will vary as a function of its orientation relative to the flow.

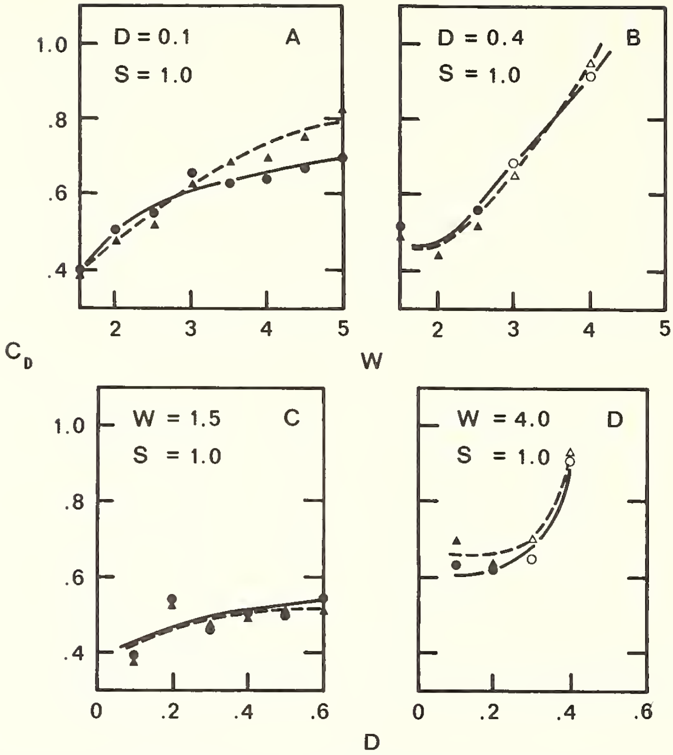
The shape of the shell (and therefore streamlining) does not change, but the position of individual morphologic elements with respect to the flow may vary substantially. Fossil cephalopods were probably able to alter their orientation in the manner of *Nautilus*, so that it is of some value to examine the effect of orientation in more detail.

TABLE 2. Difference in model drag coefficients between attitudes of 30° and calculated rest attitude. Positive values indicate C_D in rest position exceeds C_D in 30° position. Negative values indicate C_D in 30° position exceeds C_D in rest position.

W	D					
	0·1	0·2	0·3	0·4	0·5	0·6
1·5	−0·02	−0·03	+0·02	−0·02	+0·02	−0·06
2·0	−0·06	−0·06	−0·03	0·0	−0·05	
2·5	−0·09	−0·06	−0·07	−0·07	−0·09	
3·0	−0·08	−0·08	−0·03	−0·04		
3·5	+0·12	−0·04	−0·04		−0·05	
4·0	+0·13	+0·01	+0·08	+0·05		
4·5	+0·18	+0·07	+0·08			
5·0	+0·26	+0·08	+0·12			

Table 2 shows the extent of the difference between drag coefficients for orientations of 30° and calculated rest attitude (which vary between 1° and 124° depending on W and D, see Table 1). In most cases the amount of variation in drag coefficient is relatively small. Low W shells generally have somewhat lower drag coefficients in their rest attitudes, while high W shells have higher drag coefficients. No obvious trend occurs as a function of D. As shown in text-fig. 14, these differences do not significantly alter the nature of the dependence of drag coefficient on shell geometry. Compared to shell form, orientation appears to be a comparatively minor hydrodynamic factor.

Text-fig. 15 shows how drag coefficient varies as a function of attitude in low and high W shells. In both cases, drag coefficient is minimum when the aperture is aligned parallel with the flow (i.e. at 90°). Minimal drag coefficients in this configuration are probably due to: (1) virtual elimination of the aperture as a hydrodynamic factor; and (2) shell asymmetry. When the aperture is inclined at an angle of less than 90° (as in text-fig. 3A, B), truncation of the shell surface at the aperture margin forces the flow in this region to separate prematurely (Pl. 84, figs. 1, 3, and 4; and text-fig. 5A, C, D). When attitude is greater than 90°, the aperture impinges directly on the flow, and forces the flow to diverge around it (Pl. 84, fig. 2; and text-fig. 5B). In both cases, an inclined aperture results in more turbulence, and hence more total shell drag, than when the aperture is parallel. The effect of shell symmetry can be illustrated by considering a scallop shell. When a scallop is held in its normal swimming position, that is, with the commissure parallel to flow (attitude = 90°), it will disturb far less water than when the commissure is inclined to the flow (for example, commissure perpendicular; orientation = 0°). Similar discrepancies as a function of attitude should occur for coiled cephalopods because a cephalopod shell, like a scallop shell, is symmetrical in only one plane (plane of bilateral

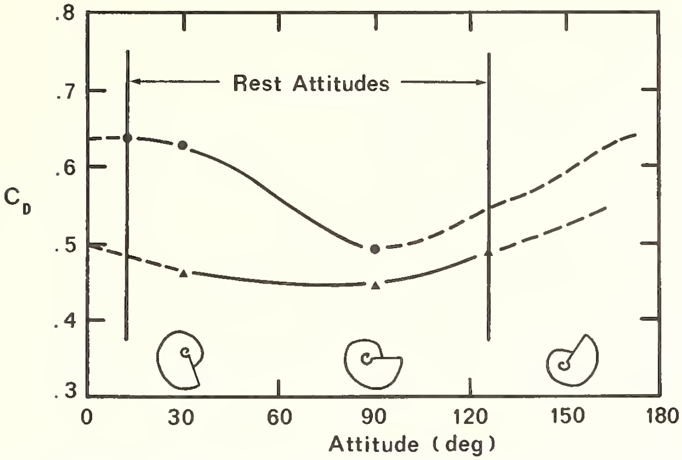


TEXT-FIG. 14. Comparison of drag coefficient (C_D) for shell models in calculated rest orientation and 30° orientation. Dots—30°, whorl onlap. Circles—30°, whorl offlap. Solid triangles—rest attitude, whorl onlap. Open triangles—rest attitude, whorl offlap. A, C_D versus W, $D = 0{\cdot}1$, $S = 1{\cdot}0$; B, C_D versus W, $D = 0{\cdot}4$, $S = 1{\cdot}0$; C, C_D versus D, $W = 1{\cdot}5$, $S = 1{\cdot}0$; D, C_D versus D, $W = 4{\cdot}0$, $S = 1{\cdot}0$.

symmetry). Rotation around the coiling axis will alter the configuration a cephalopod presents to the flow in the same way as for a scallop shell. However, the effect on drag coefficient should be much smaller in cephalopods because their low expansion rates render cephalopod shells more nearly symmetrical with respect to the axis of rotation.

The way in which drag coefficient varies in Table 2 can be explained as the result of how rest orientations differ with respect to the 30° orientation of *Nautilus*. The calculated rest attitudes of low *W* specimens are near 90° (Table 1). Drag coefficients near 90° are generally lower than at 30° as explained above, so that the drag coefficient differentials of low *W* shells are negative as illustrated in Table 2. The rest attitudes of high *W* shells are less than 30° (Table 1), and hence their drag coefficient differentials are positive (Table 2).

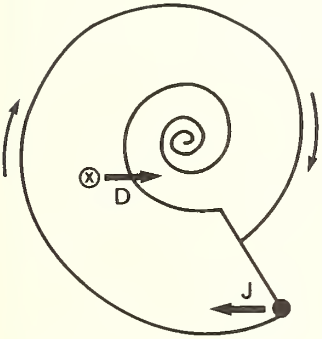
Text-fig. 15 also shows that attitudinal variation in drag coefficient is greater for high *W* shells. This probably results from the high degree of inflation characteristic of high *W* morphology. High *W* shells have large apertures and rapidly enlarging whorls, both of which make the configurations such shells present to the flow as a



TEXT-FIG. 15. Drag coefficient (C_D) versus attitude for high W (dots) and low W (triangles) shells. High W shell-model no. 14, low W shell-model no. 17.

function of orientation, and attendant flow disruption, highly variable (for cephalopods). In contrast, low W shells have relatively small apertures and whorls which expand very gradually (when $W = 1$, a logarithmic spiral decays into a circle, and shell form would become toroidal, i.e. symmetrical with respect to the coiling axis). Since low W shells are thus morphologically more uniform, attitudinal variation will have a smaller effect on drag coefficient.

The rocking associated with swimming in *Nautilus* is associated with variations in instantaneous thrust resulting from pulsations of the hyponome. Since total drag acts near the centre of the shell and thrust is applied at the ventral margin of the aperture (see text-fig. 16), the two forces set up a moment which rotates the shell away from its rest position. As thrust and drag increase, the angular rotation should increase correspondingly. Analysis of a movie film of *Nautilus* swimming supports this interpretation. The relation between lines of action and points of application of drag and thrust should be the same as that shown in text-fig. 16 as long as rest orientation lies between 0° and 90°. Since calculations on static stability (Trueman 1941; Raup 1967; J. S. Weaver, pers. comm.), and experiments on floating orientation (Reyment 1958, 1973; Raup 1973; Weaver and Chamberlain 1976) show that most coiled cephalopods probably had rest orientations within these limits (the only exceptions may have been shells with $1{\cdot}25 \leqslant W \leqslant 1{\cdot}75$, Raup 1967), it appears that most shells must rotate like *Nautilus* during swimming. Thus it follows that the lowest effective drag coefficient of a cephalopod shell (with the above exception) will be that measured in its rest position



TEXT-FIG. 16. Effect of drag and thrust on attitude. Shell moving from right to left. Drag (D) acts backward from centre of dynamic pressure (⊗), which lies near centre of gravity near coiling axis. Thrust (J) acts in direction of motion from point of application (●) at ventral margin of aperture. Lines of action of the forces set up a moment which causes a clockwise rotation of the shell (arrows).

because rotation during swimming always alters attitude (text-fig. 16) in the direction of greater drag coefficient (text-fig. 15). Therefore the faster an ammonoid or nautiloid swam, the more closely its attitude must have approached 0°, and the greater its effective drag coefficient would have become. This in itself may have placed upper limits on the performance of fossil cephalopods, especially those with low drag coefficients (e.g. involute oxycones).

CONCLUSIONS

Tow-tank measurement of shell drag coefficient (C_D), and flow visualization of shell flow patterns suggest the following:

1. Flow around coiled cephalopod shells is characterized by three kinematic properties:
   (*a*) boundary layer separation along the flank of the outer whorl approximately coincident with the outer umbilical shoulder;
   (*b*) a turbulent wake behind the shell caused by separation;
   (*c*) turbulent, unsteady vortices in the umbilicus.

2. Low drag coefficients are produced by shell morphologies which delay separation, and generate little turbulence. Shell drag coefficient is nearly independent of velocity for Reynolds numbers less than about 3×10^5, and in this respect is comparable to drag coefficients of other blunt, rounded bodies in subcritical flow.

3. The following trends in drag coefficient occur as a function of expansion rate (W) and umbilical size (D) in shells with roughly circular whorl sections:
   (*a*) C_D increases from about 0·45 in low W (deflated) shells to 0·9 in high W (inflated) shells;
   (*b*) C_D generally increases with D (i.e. as umbilicus enlarges);
   (*c*) whorl offlap results in comparatively high $C_D (\approx 1{\cdot}1)$.

4. Variation in whorl compression (S) causes order of magnitude changes in drag coefficient. Involute oxycones ($D < 0{\cdot}1$; $S \approx 0{\cdot}2$) probably have the lowest $C_D (\approx 0{\cdot}1)$ of all cephalopod shells. Depressed cadicones ($S > 1$) have high $C_D (\approx 1{\cdot}0)$. While gross change in shell form may not greatly affect C_D when S is high ($S \approx 1$), the C_D's of low S (compressed) shells are very sensitive to changes in morphology.

5. Drag coefficients of cephalopod shells are more than an order of magnitude higher than the drag coefficients of the bodies of rapid-swimming fish, mammals, and squids. This means that even the best streamlined shelled cephalopod (involute oxycone) is at least ten times more inefficient than these animals. Depressed cadicones are probably more than 100 times less efficient.

6. Decrease in drag coefficient as a function of increasing whorl compression is due to increasing gentleness of the surface curvature of the shell, and to removal of the position of maximum shell width backward from the leading edge of the shell. Increase in drag coefficient with W is due to increase in frontal area and relative size of the aperture. Increase in drag coefficient with D is due to increase in the size of the umbilicus.

7. Drag coefficient varies with shell orientation because shells are not morphologically uniform in three dimensions. The lowest drag coefficients occur when the aperture is orientated parallel to the flow and increases as the aperture rotates away from this position. The magnitude of this increase is greatest in high *W* shells. However, the over-all change in drag coefficient is relatively minor compared to variation due to shell form. For most shells the rotational moment due to drag and thrust is such that the lowest effective drag coefficient occurs when shells are orientated in their rest position. This implies that drag coefficient increases with swimming speed.

8. Analogy with ship and aircraft appendages suggests that extension of the body behind the shell has virtually no effect on drag coefficient for most ectocochliates.

Like any high performance machine, rapid swimmers must be efficient. They do not waste their limited supply of propulsive energy in unproductive ways. Their bodies are well streamlined because such shapes have the highest hydrodynamic efficiencies. Inasmuch as body shape and swimming ability are so closely related, understanding the hydrodynamic properties of shell form is an important step toward deducing the swimming ability and life habits of fossil cephalopods.

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THE ANALOGUE VIDEO RESHAPER—A NEW TOOL FOR PALAEONTOLOGISTS

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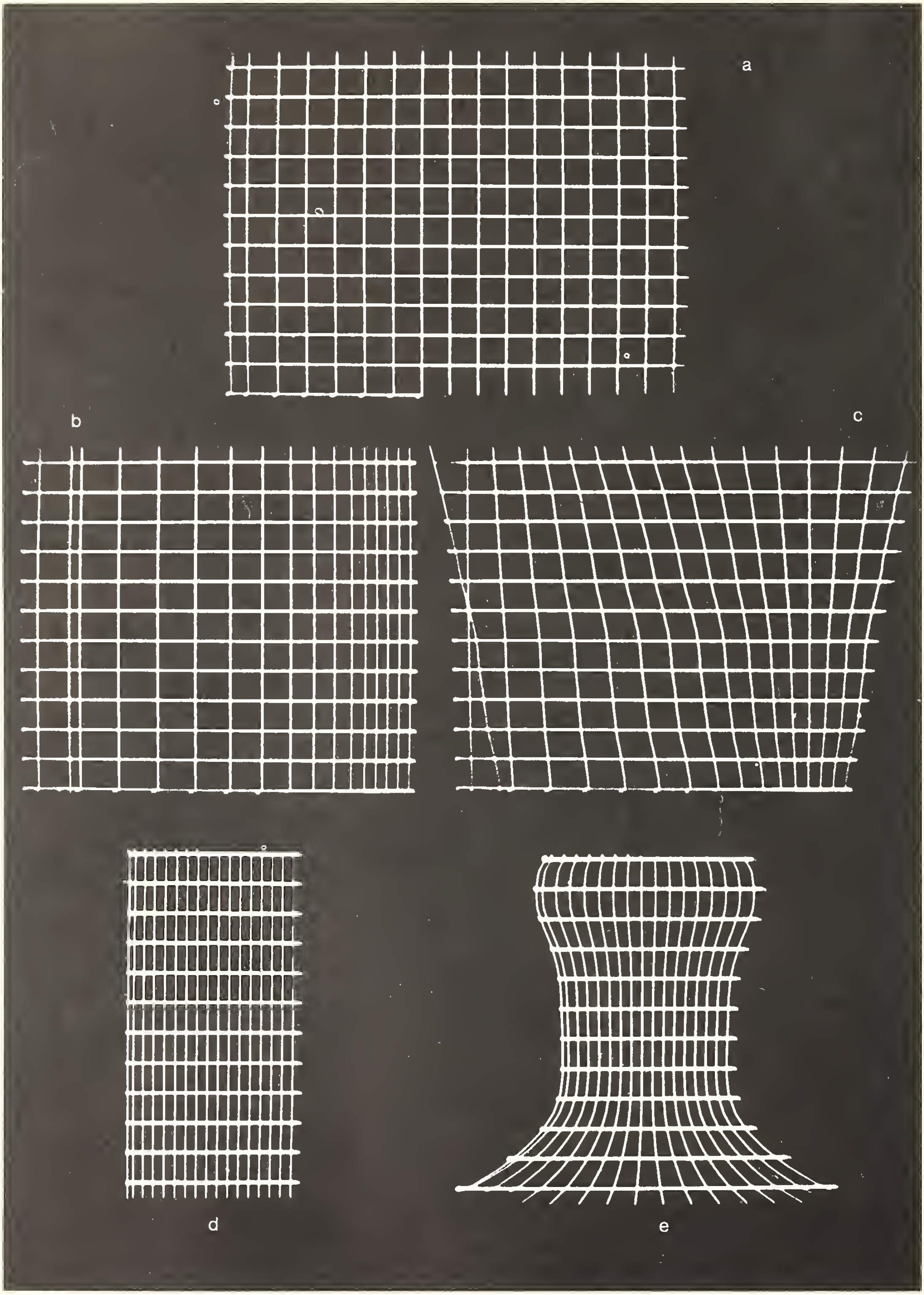
ABSTRACT. A television-based system has been devised to overcome two classes of problem, crushing and distortion, and subjectivity in choice of features to be compared. The system is an automation of D'Arcy Thompson's method of transformation. Removal of the effects of shear is demonstrated from *Angelina*. Other illustrations comprise intraspecific variation in *Chlamys varia* (Linnaeus) and *Goniorhynchia boueti* (Davidson), variation in *Micraster*, ontogenetic variation in the reptile *Stenopterygius quadricissus* (E. Fraas), and phylogenetic variation in a group of closely related hominids. The system has proved more sensitive and quicker than existing practices and although no attempt is made to solve any specific problem, suggestions for discussion are raised.

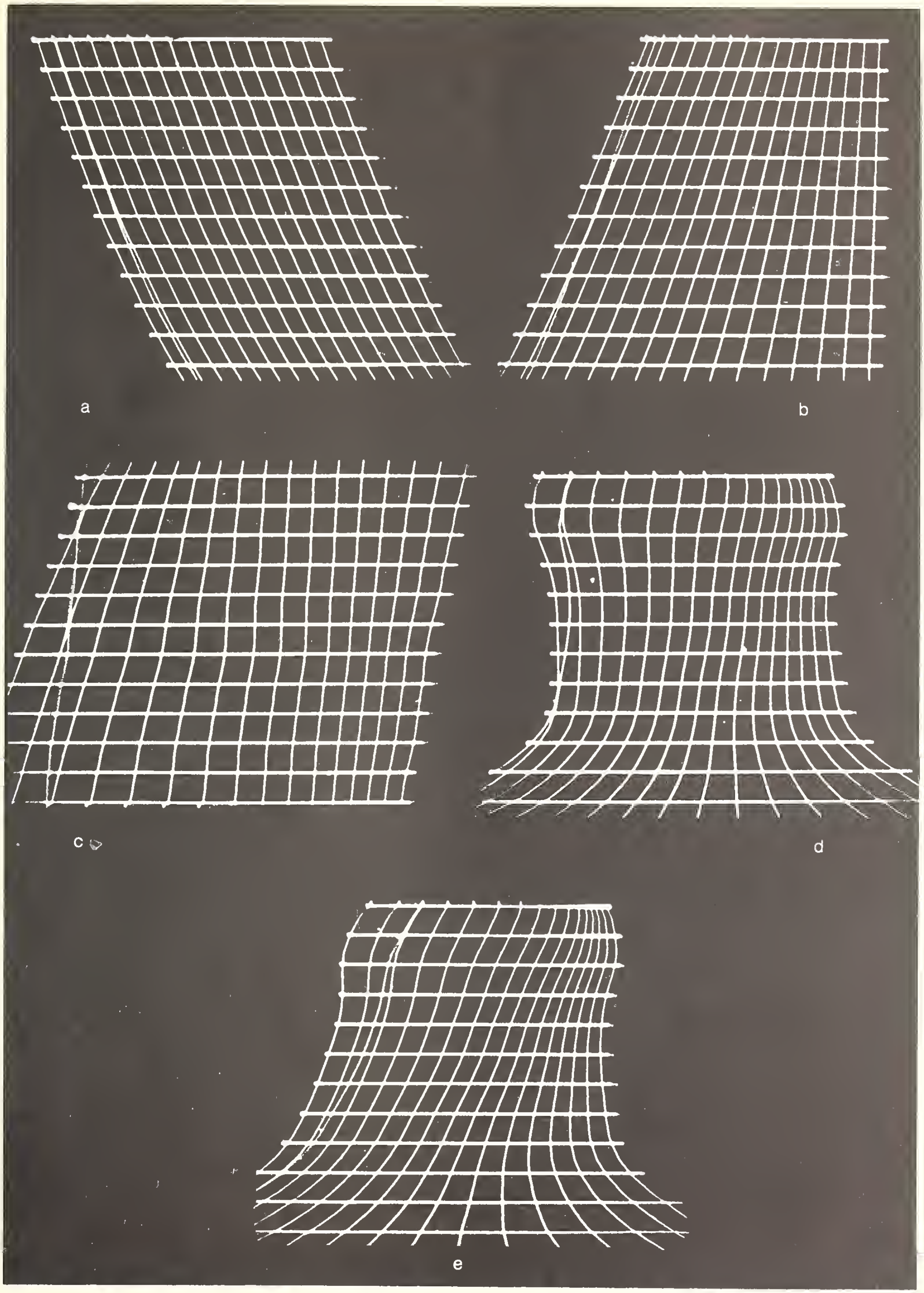
THE palaeontologist often faces two problems, first, having to work with crushed and deformed material and, secondly, subjectivity in his choice of parameters to be described, measured, and weighted. Both may lead to unconscious bias and error in resulting comparisons. Until recently no method of making rapid accurate restorations of deformed or crushed fossils was known, but various methods of comparing organisms have been devised and used over the years. By far the most ingenious and productive of these is the graphical method of Thompson (1917) known as the method of transformations. This method is a modification of the way an artist enlarges a drawing. The artist places a rectilinear grid over the subject to be enlarged. He then draws a grid of the requisite size and redraws the subject so that it occupies the same relative position on the enlarged grid. D'Arcy Thompson placed the grid on the first form and then redrew the grid over the form with which it was to be compared, so that the grid was modified to pass over similar or homologous points on the second form. Although the two subjects were often complex, the resulting modified grid was relatively more simple and also capable of more complete mathematical analysis.

Thompson's method was the first to encompass the comparison of all the features and measurable quantities in a two-dimensional view in one operation, but other kinds of methods have been devised to increase the scope of comparisons. Olson and Miller (1958) found that the closer the correlations between sets of measures (ρ-groups), the more recognizable the functional sets (F-groups) among the parts measured. The results are expressed as correlation diagrams between the measures, but these unfortunately remove the pictorial appreciation of the dispositions of the functional groups in the organisms. The method also tends to reduce the recognition of the possible evolutionary value of loosely correlated but consistently present sets of measures. Although the assembling of data by this method is laborious it is susceptible to digital treatment. Other palaeontologists believe that equations may be written for the totality of shape information representing the organism. Using such equations, digital comparisons with other organisms should then be possible but this is a very difficult procedure, requiring expensive hardware and much time. Results have yet to be published.

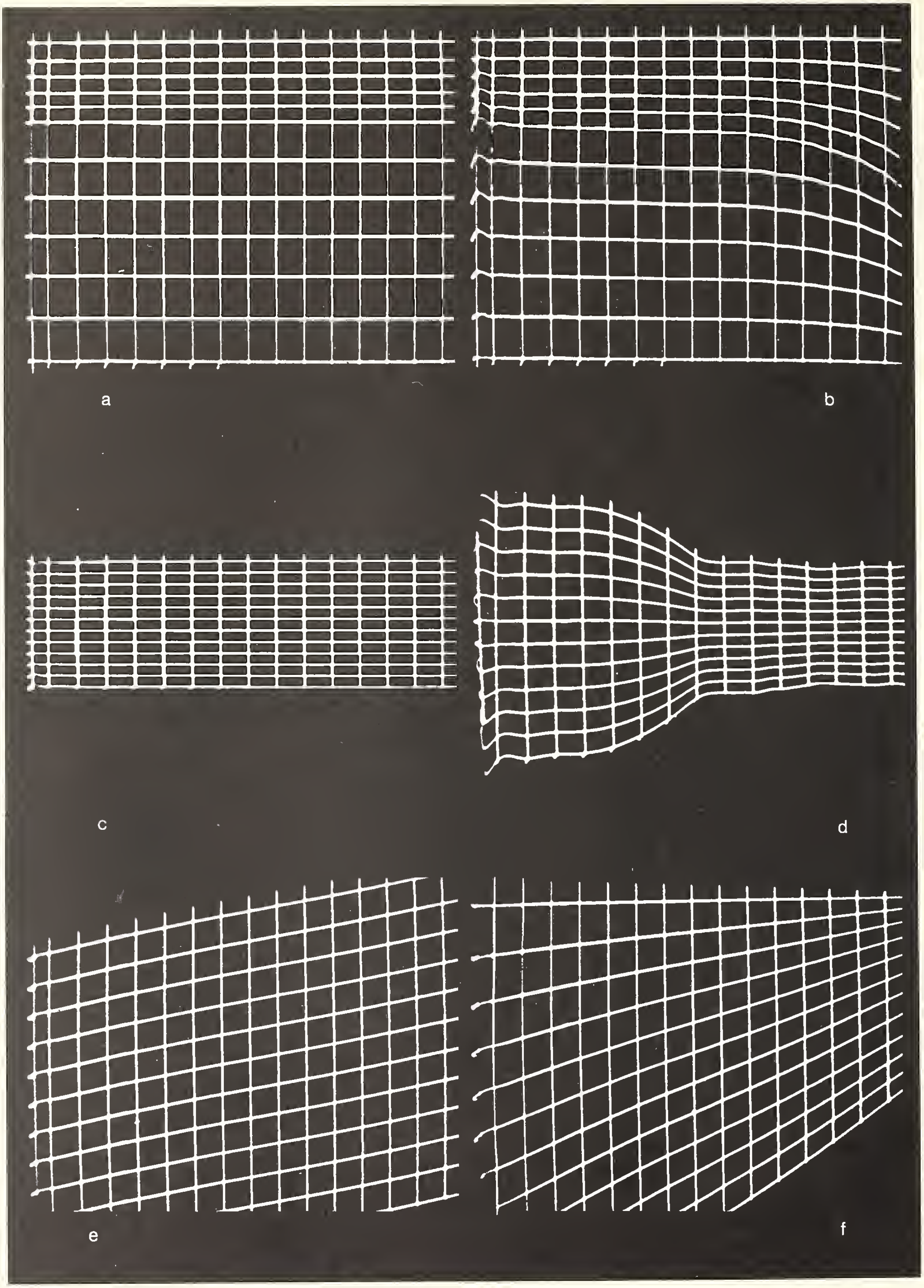
[Palaeontology, Vol. 19, Part 3, 1976, pp. 565-586, pls. 85-91.]



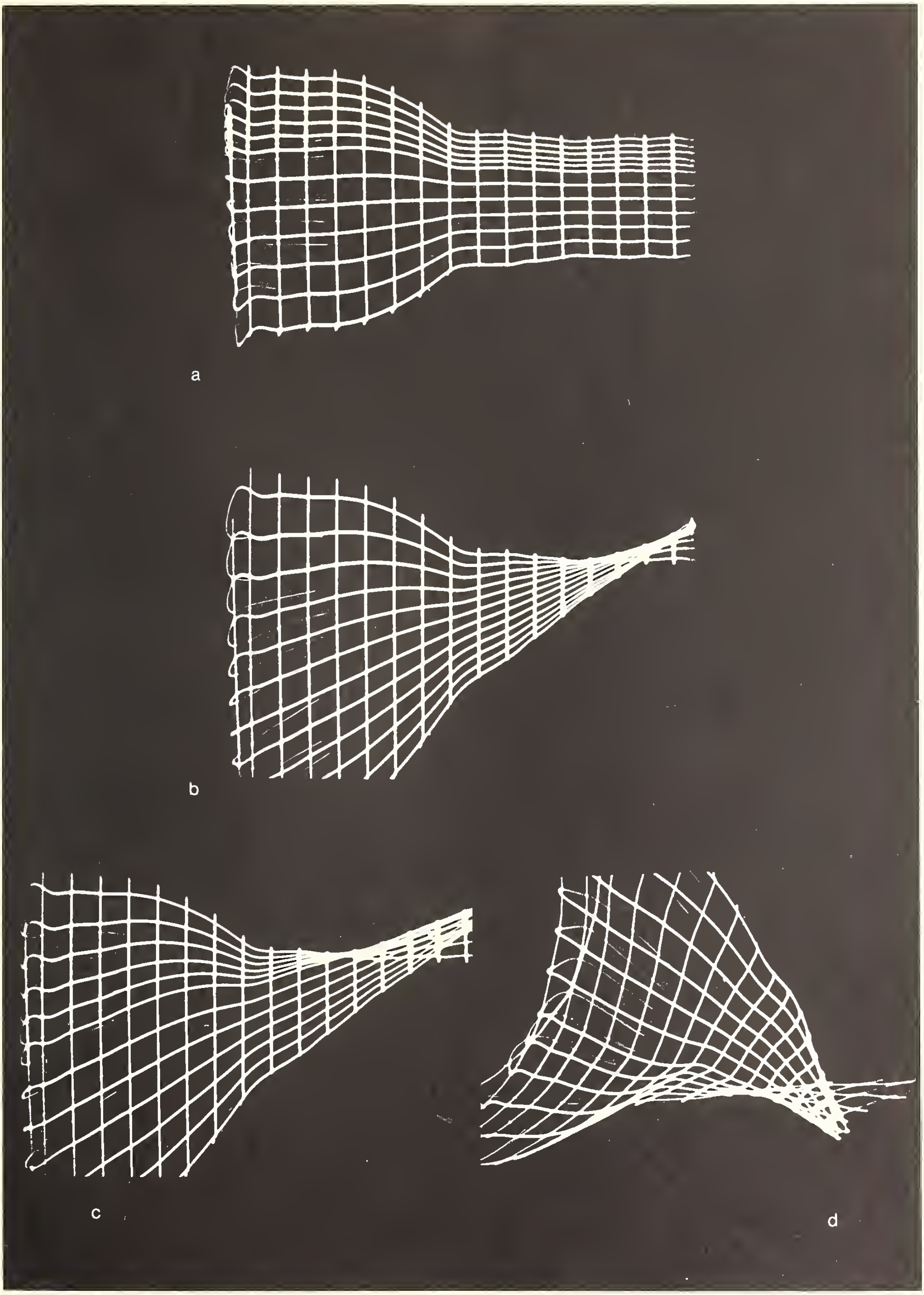
TEXT-FIG. 1. Figs. *a–e*. Illustrations of electronically generated grids. *a*, unmodified rectilinear grid. *b*, grid showing horizontal non-linearity. *c*, as for fig. *b* but with down-screen modification of the horizontal non-linearity. *d*, grid showing reduction of amplitude horizontally. *e*, as for fig. *d* but with down-screen modification of the horizontal amplitude.



TEXT-FIG. 2. Figs. *a–e*. Further illustrations of electronically generated grids. *a*, grid showing horizontal tilt with some curvature introduced. *b*, as for fig. *a* but with down-screen modification of degree of horizontal tilt. *c*, combination of text-fig. 1, fig. *c* and text-fig. 2, fig. *b*. *d*, combination of text-fig. 1, fig. *c* and text-fig. 1, fig. *d*. *e*, combination of text-fig. 1, fig. *c*, text-fig. 1, fig. *e*, and text-fig. 2, fig. *b*. All horizontal variations with their down-screen modifications are illustrated in this figure.



TEXT-FIG. 3. Figs. *a–f*. Further illustrations of electronically generated grids. *a*, grid showing vertical non-linearity. *b*, as for fig. *a* but with across-screen modification of vertical non-linearity. *c*, grid showing reduction of amplitude vertically. *d*, as for fig. *c* but with across-screen modification of vertical amplitude. *e*, grid showing vertical tilt of original rectilinear grid. *f*, as for fig. *e* but with across-screen modification of the degree of tilt.



TEXT-FIG. 4. Figs. *a–d*. Further illustrations of electronically generated grids. *a*, combination of text-fig. 3, fig. *b* and text-fig. 3, fig. *d*. *b*, combination of text-fig. 3, fig. *d* and text-fig. 3, fig. *f*. *c*, combination of text-fig. 3, fig. *b*, text-fig. 3, fig. *d*, and text-fig. 3, fig. *f*. *d*, combination of text-fig. 2, fig. *e* and text-fig. 4, fig. *c*. This is an example of the combination of all horizontal manipulations with their down-screen modifications together with all vertical manipulations with their across-screen modifications.

But alongside these new approaches, the original Thompson method has continued to interest palaeontologists and other scientists. It served as a starting-point for Huxley's (1932) work on allometry, while Harris (1947) suggested that the method might be used to investigate problems in genetics. Other users include Lull and Gray (1949) on growth in ceratopsians, Langston (1953) on Permian amphibians, and Chatterjee (1974) on rhynchosaurs. Simpson *et al.* (1960) regarded it as a 'very interesting way of making similar comparisons in greater detail and taking into account areas and angles or directions as well as linear dimensions', and Sokal and Sneath (1963), recognizing both its value and its time consuming nature, called for automation of the method of transformations. Blackith *et al.* (1963) discussed the use of transformation grids in the study of growth and form, while Bliss (1958) and Lu (1965) applied Fourier analyses to the grids. Sneath (1967), using third-order curves, and Cooper (1965), using quadratic discriminant functions, have both examined pattern recognition with respect to deformed grids.

However, it is not the purpose of this paper to discuss the mathematical treatment of grids or the directions of development of numerical methods which are described in detail in many papers and books such as Clark and Medawar (1945); Simpson *et al.* (1960); Sokal and Sneath (1963); Sneath (1967); Smirnoff (1963, 1968, 1969); and Blackith and Reyment (1971). The object of this paper is to describe, with examples, a rapid and accurate way of performing Thompson's transformations, using a new television method. It is more accurate than the work of the artist, it is relatively cheap, and it enables libraries of grids to be produced quickly.

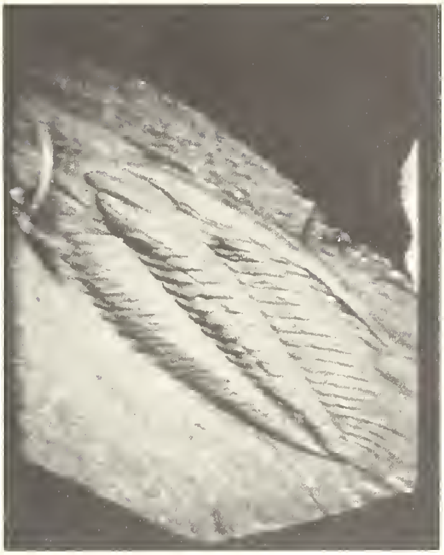
DESCRIPTION OF THE ANALOGUE VIDEO RESHAPER (AVR)

The fundamental principle of the system is controlled distortion of the basic rectangle of the television picture. Non-linearity (of any chosen type) may be introduced, both vertically and horizontally, the size of the picture may be contracted or expanded horizontally or vertically, and the picture may be tilted into parallelograms, trapezia, or other shapes, some curved, in both horizontal and vertical directions. Controls are also built in so that the modifications may be altered at will in separate parts of the picture.

Using these facilities, a still television picture of an animal viewed by television camera A, may be modified until it fits a static picture of another animal, viewed by television camera B, which remains on the screen while the match is being made. An electronically generated rectilinear grid may be superimposed on the picture being fitted which is automatically modified at the same time. The resultant picture on the screen is of two animals matched together, with a modified grid superimposed, the whole of which is similar to Thompson's transformations. Switching may be used to give any combination of either picture and either grid. Both the picture and the rectilinear grid may be switched out so that the modified grid alone remains.

EXPLANATION OF PLATE 85

Figs. 1-4. Removal of shear from *Angelina* (×1$\frac{1}{3}$). 1, *Angelina* as collected (National Museum of Wales No. 27-110-G836). 2, the same with the electronic rectilinear grid superimposed. 3, the specimen restored to bilateral symmetry. 4, the restored specimen with the deformed electronic grid superimposed enabling the shear angle to be measured.



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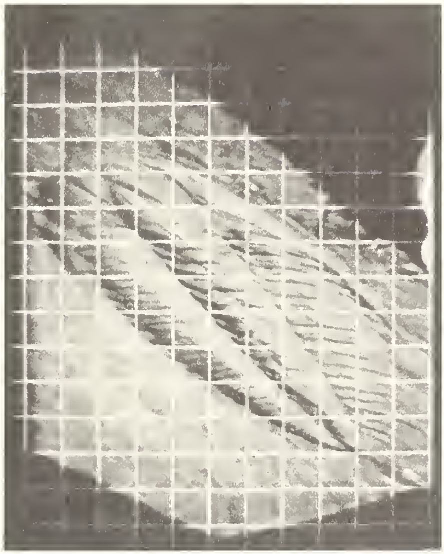

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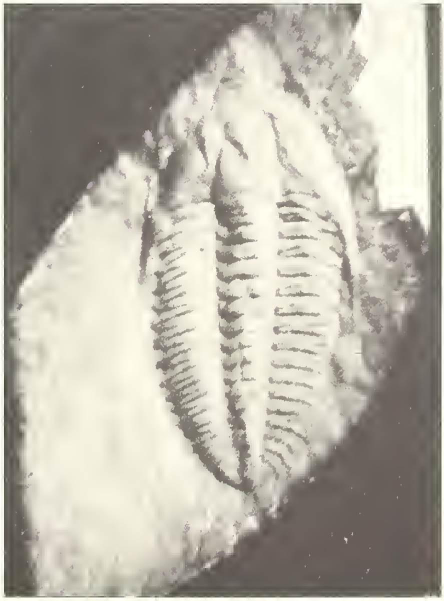

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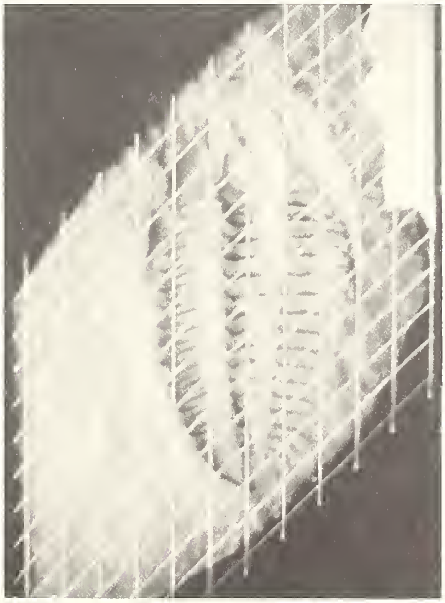


4

APPLEBY and JONES, *Angelina*

Text-figs. 1–4 show a sample of each kind of grid. It is often desirable to standardize one principal dimension common to both subjects so that, when they are displayed on the cathode ray tube prior to comparison, they are covered by identical grids. This ensures that the length of each square in the grid is the unit of measurement for both pictures. If during a match a square is distorted, it is easy, using calipers, to determine its relationship to the size of the original square.

The apparatus, excluding the television cameras and associated lighting, is of desk-top size, and for those who are interested in the detailed electronic engineering a technical account is given in Appleby and Jones (1972). No programming or knowledge of electronics is required to operate the AVR. The principles of operation may be demonstrated in a few minutes and after a short learning period for each different research project, the operator can exploit the full capacity of the system.

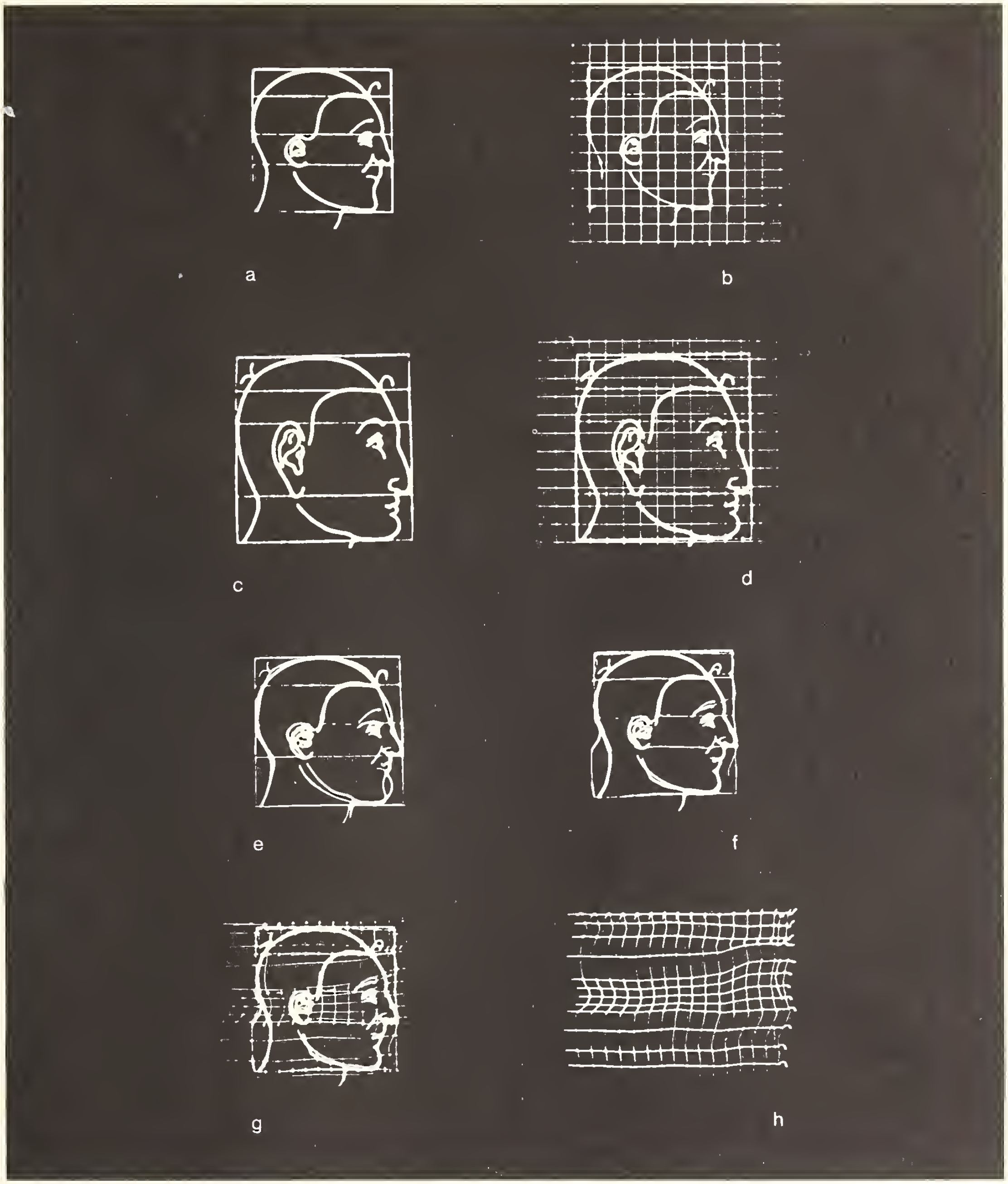
EXAMPLES

None of the following examples is intended to be a study of a particular problem in any depth but is intended to show the scope of the system. Advantages of the system are many: it handles specimens, half-tone photographs, and line-drawings equally well; crushing may be removed quickly in many cases; operation is rapid. The system will probably lead to a feasible new approach to statistical treatment of complex objects (e.g. Sneath 1967), and will make easier studies of morphology, growth, and evolution. Only those forms which possess a predominantly radial symmetry present difficulties, although these are not insuperable using the present system. A projected polar version will enable these to be processed with greater ease.

The examples given below illustrate part of the range of groups and taxonomic ranks already processed by the system.

Comparisons with material used by Thompson

A test was carried out on one of Thompson's (1917) illustrations, a set of line-drawings after Dürer, of human heads seen from the right. Thompson used them to illustrate the effect of applying a vertical non-linearity to the human head and to compare the results with an apparently 'average' head. For the average head (text-fig. 5, figs. *a*, *b*) the guide lines given were three lines drawn horizontally from front to back of the head at approximately equal intervals down the drawing. Text-fig. 5, fig. *b* shows this with a square grid superimposed. For the second drawing (text-fig. 5, figs. *c*, *d*), these lines were spaced unequally and the face redrawn. It looks quite different. In order to check the accuracy of the second drawing with the AVR, the new face, drawn over the non-linearly spaced lines, was placed before a television camera and the lines were returned and matched to their original and more regularly spaced positions (text-fig. 5, fig. *e*). Interestingly, the original face was not very accurately re-created due to artist's error, but using the AVR the 'new' face was accurately superimposed over the 'average' one. The results may be seen in text-fig. 5. The superimposed electronic grid (text-fig. 5, fig. *g*) and the grid alone (text-fig. 5, fig. *h*) show that the artist was largely right in his use of non-linearity down the face, but that he had failed to apply less modification to the region of the eye and nose than to the rest of the head.



TEXT-FIG. 5. Figs. *a–h*. Comparisons of heads by Dürer which were used by D'Arcy Thompson to illustrate the method of transformations. *a*, an 'average' head, from D'Arcy Thompson after Dürer. *b*, the same with a rectilinear grid superimposed. *c*, second head from D'Arcy Thompson after Dürer with the middle part of the head expanded. *d*, the head as in fig. *c* but with a rectilinear grid superimposed. *e*, the second head matched to the 'average' one using D'Arcy Thompson's criteria. *f*, the second head superimposed on the 'average' one using only the contours of the heads. *g*, as for fig. *f* but with the electronic grid superimposed to indicate the modifications used to make the match using this method. *h*, the modified grid alone.

Removal of the effects of shear

A simple example of the use of the system for uncrushing fossils is the removal of shear from the trilobite *Angelina* (Pl. 85, figs. 1–4). The specimen was mounted before the television camera and photographed (Pl. 85, fig. 1). A rectilinear grid was then switched in and a photograph taken (Pl. 85, fig. 2). The grid was then switched out, the trilobite returned to bilateral symmetry, and the grid switched in again. Photographs were taken at each stage (Pl. 85, figs. 4, 5). The removal of the distortion took approximately five seconds. A further advantage of the system shown by this example is its relationship to shearing in the rock. The fossil is in a matrix in which lineations which are related to shear directions are present. These disappear from the screen when the shear is removed from the fossil. The lineation angle may be measured accurately from the photograph of the modified grid. There is probably a future for the use of the system using lineations only, when fossils are absent.

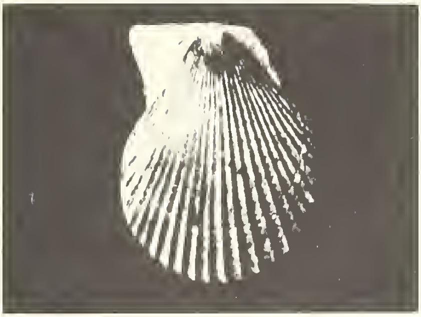
Infraspecific variation

(*a*) Two specimens of *Chlamys varia* (Linnaeus) valves were collected from the beach at Aberavon, South Wales, and brought to the same dorsoventral length before the television cameras and subjected to the AVR matching process. In Plate 86, figs. 1, 2 the smaller of the two valves is shown with and without the square grid. In Plate 86, figs. 3, 4 the larger of the two valves is similarly illustrated. The difference of size between the two shells is 0·7 cm, measured at their maximum dorsoventral heights. The shells are slightly worn because they were separated valves collected after a limited period of reworking on the beach. In spite of the small size difference between them, other differences could be seen when the smaller and presumably younger shell was matched to the larger shell (Pl. 86, fig. 5), especially when the modified grid was switched in (Pl. 86, fig. 6). The greatest difference is on the posterior side, but in the hinge and ear region the smaller specimen has been contracted relatively to fit the larger. Measurement with calipers shows that there is no relative elongation of the ears at the hinge. The calipers also show that although the anterior side is also expanded dorsoventrally, it is also expanded anteroposteriorly, giving the grid a more rectilinear appearance. The differences between these two variants of the one species *C. varia* bring out the need to compare not only large numbers from a fossil assemblage but also the need, where the structure of the shell permits, for comparison of growth series to be made using deformed grids in order to compare growth patterns statistically. Digital read-out followed by a version of the trend-surface analysis described by Sneath (1967) would together increase the accuracy and speed of this process.

(*b*) Two specimens of *Goniorhynchia boueti* (Davidson) from the Great Oolite Clays (Jurassic) at Langton Herring, Dorset, were examined using the apparatus.

EXPLANATION OF PLATE 86

Figs. 1–6. Comparison of two specimens of *Chlamys varia* (Linnaeus). 1, the smaller specimen unmodified (×0·95). 2, the same with the rectilinear grid superimposed. 3, the larger specimen unmodified (×1·1). 4, the larger specimen with the rectilinear grid superimposed. 5, the smaller specimen matched to the larger one. 6, the matched specimens with the modified grid of the smaller specimen superimposed.



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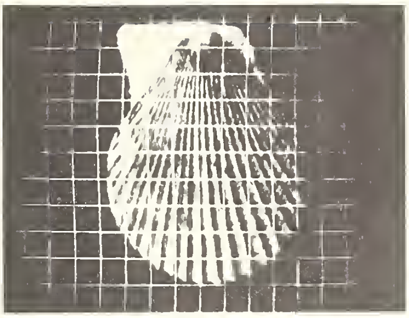

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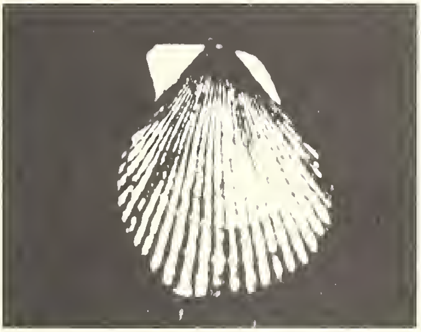

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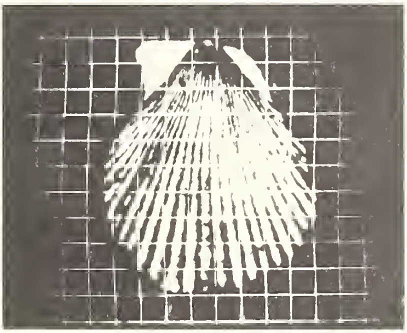

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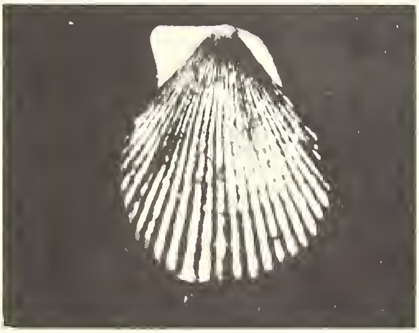

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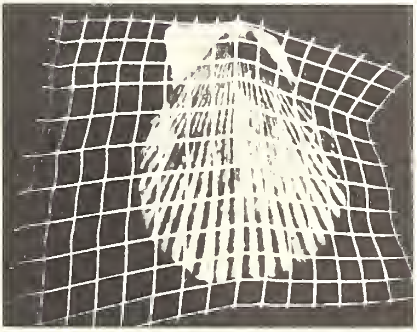

6

APPLEBY and JONES, *Chlamys*

The locality is the same as Aitken and McKerrow's (1948). Both belong to Series 2 of Aitken and McKerrow and closely resemble the individual 'G' in plate 2 of their paper. The two individuals were selected for comparison because of their uncrushed appearance and because they had slightly different shapes and sizes. The smaller of the two has a small piece of matrix attached to one end of the commissure. Both were brought to uniform width before the television cameras, the piece of matrix giving rise to a possible error estimated at no more than 3%. As may be expected when a more inflated specimen is fitted to a less inflated one brought to the same breadth, the modified grid shows contractions in various areas but it is interesting to note the nature of the modifications as a whole. There are three categories: areas of contraction, absence of contraction, and expansion areas which show that the specimen being modified is relatively smaller in these areas or directions. The unaffected part of the grid shows that the sulcus area remains almost constant in spite of the size differences while the rest of the specimen above and lateral to the sulcus contracts dorsoventrally. The maximum breadth remains the same when rearranged but lateral expansions occur above and below this level, showing that the smaller specimen had to be expanded laterally in these regions to fit the larger specimen.

The difference between these two specimens is opposite to the findings of Aitken and McKerrow who found that, in general, the breadth and thickness of *G. boueti* increase more rapidly than the length with growth. Here the smaller specimen is the thickest. Possibly this pair represent phenotypic variation which happens to run counter to the statistical trends. Alternatively, the larger specimen is more crushed dorsoventrally than the smaller one. In order to check the second possibility, the whole of the University College, Cardiff collection of this species from the locality was examined. Of the 474 specimens which were sufficiently whole, over 55% were found to be crushed and distorted. In cases of doubt, the doubtful specimens were added to the 'uncrushed' ones. Any bias is therefore against the hypothesis of crushing. The direction of crushing in the Cardiff collection is predominantly dorsoventral, suggesting that there was a preferred orientation of these shells in the bed from which they came. Compaction, possibly very slow, of the muddy sediments in which they occurred is a possible cause of the crushing. That the Langton Herring material does not represent an originally living assemblage *in situ* is suggested by the absence of very small individuals. This suggests sorting during transportation, and the fact that some of the serpulids reported by Aitken and McKerrow (1948) cross the closed commissure in several individuals denotes that the brachiopods lay dead upon the bottom while the tubes were secreted.

The comparison of the two specimens used to illustrate the method shows that the *boueti* question could be re-examined with crushing in mind. For instance, does

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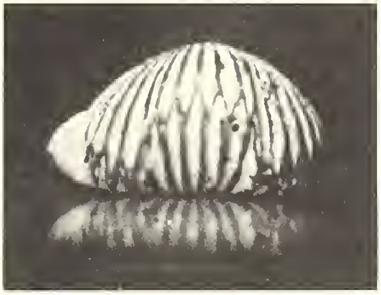
EXPLANATION OF PLATE 87

Figs. 1–7. Comparison of two specimens of *Goniorhynchia boueti* (Davidson). 1, the smaller specimen unmodified (× 1·52 approx.). 2, the same with rectilinear grid superimposed. 3, the larger specimen unmodified (× 1·38). 4, the larger specimen with rectilinear grid superimposed. 5, the smaller specimen matched to the larger. 6, the match with the modified grid superimposed. 7, the modified grid alone.



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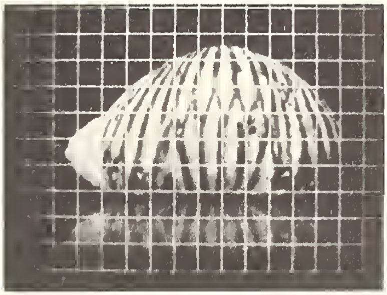

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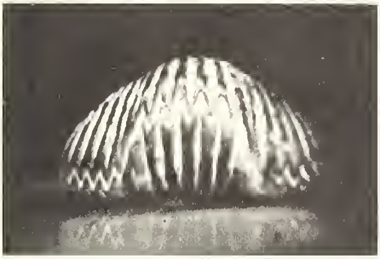

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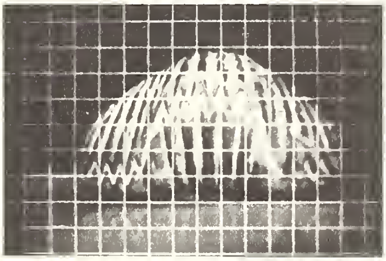

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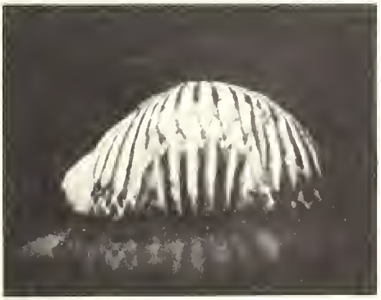

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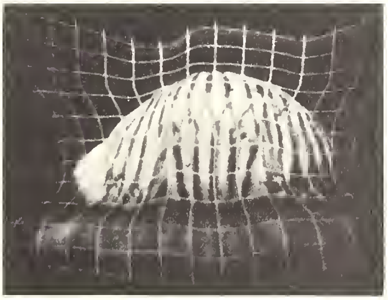

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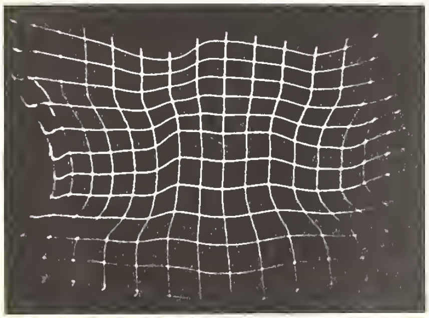

7

APPLEBY and JONES, *Goniorhynchia*

the pair compared perhaps indicate that the sulcus is the last part of the anterior part of the shell to give way under increasing crushing? If so, many thinner forms with more widely splayed sulci may not reflect growth characteristics alone.

Micraster

Two Cretaceous echinoids, *Micraster corbovis*, a low zonal type, and *M. coranguinum*, a higher zonal type, were used to demonstrate the technique in use with echinoids. The lower zonal *M. corbovis* (Pl. 88, figs. 1, 2) was matched to the higher *M. coranguinum* (Pl. 88, figs. 3, 4). A good match was reached very rapidly (Pl. 88, fig. 5) and the grid is shown superimposed upon the match and alone in Plate 88, figs. 6, 7 respectively. The two unmodified specimens had been brought to the same length before matching. The modified grid is less variable vertically than horizontally although a relative contraction occurs in the region of the apical disc and below it. This may equally well be interpreted as an expansion posteriorly and anteriorly since the smaller *M. corbovis* has been scaled before matching.

The more important changes occur laterally. The lower zonal form is contracted by as much as a third in the region in front of the apical disc at the level at which the petaloid abulacral areas cease. Posteriorly the elements of the modified grid expand correspondingly. This is in accordance with the posterior shift of the apical disc as set out by Nichols (1959). The modifications between these two forms reveal no new problems, the differences being intimately associated with the verbal and numerical descriptions which have been made from time to time of this group of heart urchins. The main value of the grid in this case is the added impression of the integrated nature of the group as it evolved in accordance with the controlling factors such as depth of burrowing and the migration of the anus to the posterior position. Other views would presumably show the same orderliness but sufficient has been done to show how the system may be applied to echinoids in general.

Variation in the ichthyosaur Stenopterygius

In this example, two specimens of *Stenopterygius quadricissus* (E. Fraas) from the Lias Epsilon 11_4 of Holzmaden, Germany, were scaled to the same length and compared. The smaller (Pl. 89, figs. 1, 2) is 62·5 cm long and the larger (Pl. 89, figs. 3, 4) is 115 cm long. The smaller specimen was matched to the larger and the match is shown with and without the grid superimposed (Pl. 89, figs. 5, 6). The grid alone is shown in Plate 89, fig. 7. Little attention was given to matching the fore limbs because one of these is much displaced in the smaller specimen. The most obvious difference is the general dorsoventral and anteroposterior expansion which is smallest at the head and largest posteriorly. Since this corresponds with an increase in length it is reasonable to correlate it also with the age difference of the two ichthyosaurs. At the next level of detail, the match and the modified grid over it show that

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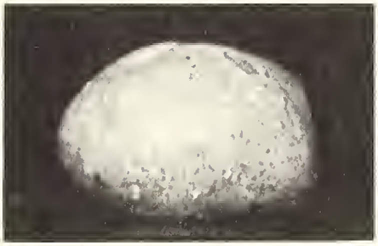
EXPLANATION OF PLATE 88

Figs. 1–7. Comparison of two forms of *Micraster*. 1, *M. corbovis* unmodified (×0·79). 2, *M. corbovis* unmodified and with rectilinear grid superimposed. 3, *M. coranguinum* unmodified (×0·62). 4, *M. coranguinum* unmodified with rectilinear grid superimposed. 5, *M. corbovis* matched to *M. coranguinum*. 6, *M. corbovis* matched to *M. coranguinum* with modified grid superimposed. 7, the modified grid alone.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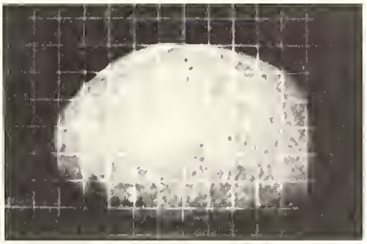
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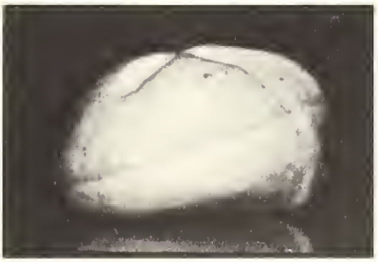
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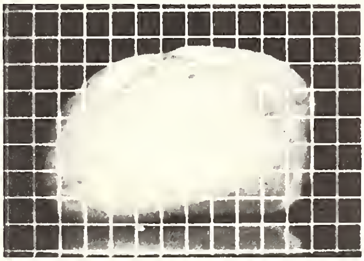
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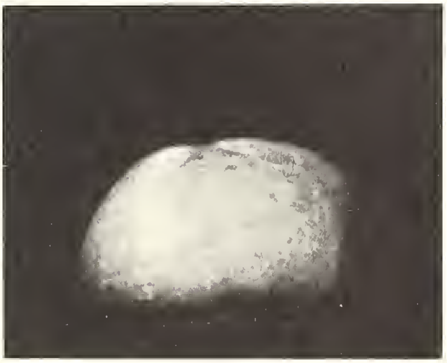
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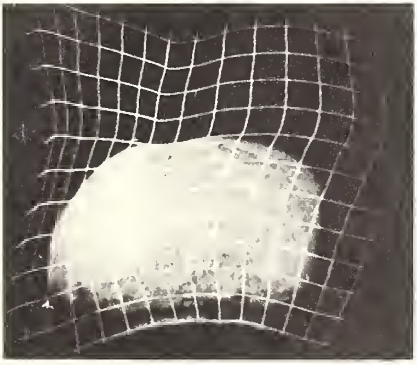
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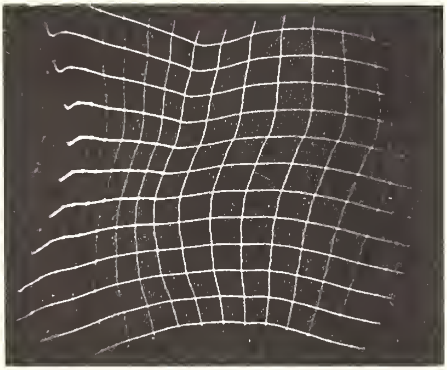
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APPLEBY and JONES, *Micraster*

as the smaller specimen grew, the changes were not uniform. The body behind the skull lengthens and deepens in the dorsal-fin region, the shoulder and caudal regions expand even more, particularly posteriorly, while the posterior dorsal and pelvic regions show minimum expansion. An apparent lack of expansion in the tail-fluke region may be due to different positions of the tail at death. The most important results of measurements, taking the length of the unmodified square as unit of length, are the almost complete absence of absolute contraction or expansion in either horizontal or vertical directions in the orbital region and the absence of posterior growth in the region of the pelvic girdle. In the latter region there is only dorsoventral expansion which is increasing into the caudal region.

The results show general similarities to von Huene's (1922) and McGowan's (1973) findings. McGowan, using three different numerical methods, inferred growth patterns in three species of ichthyosaurs, one of which is *S. quadricissus*. The methods depended on the statistical treatment of chosen variates using the allometric equation $y = bx^a$, ultimately derived from Huxley (1932). The AVR results follow the treatment of surfaces and indicate that relative growth patterns over the whole of the postcranial area are more complex and subtle than normal allometric studies indicate. An examination of von Huene's sketches of a growth series in *S. quadricissus* (von Huene 1922) shows considerable variation in postcranial body proportions and McGowan has superimposed outline drawings taken from Hauff (1953) and BMNH R.4086. These also indicate differences of postcranial dimensions, some of which are mentioned in his paper. Principal among these are tail features and dorsal-fin features. Areas of both tail fin and dorsal fin, expressed as ratios to precaudal body length for a number of specimens, and the higher correlation coefficients for these two features, are reflected in the AVR grid modifications in these areas shown in Plate 89, fig. 6. The lower correlation coefficient for the relationship between the angle of the tail-bend and body length may be due to a combination of a number of factors including developmental increase and greater flexibility in the young as mentioned by McGowan. The peduncle was certainly narrower in the smaller specimens but whether the flexibility was due to the position at death, post-mortem contractions, or later disturbance cannot be decided easily.

Comparison of possible relatives

In contrast to the matching of growth stages in one species, a comparison of relatively closely related hominoids may be made from the series shown, from *Proconsul*, through *Australopithecus*, *Pithecanthropus* (Java man), *Pithecanthropus* (Pekin man), *Homo neanderthalensis* to *H. sapiens* (Cro-Magnon man), in stratigraphical order (Pls. 90, 91). There is no intention here to indicate the precise course

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EXPLANATION OF PLATE 89

Figs. 1–7. Comparison of two growth stages of *Stenopterygius*. 1, *S. quadricissus* (E. Fraas) 62·5 cm long. 2, the same with rectilinear grid superimposed. 3, *S. quadricissus* 115 cm long. 4, as for fig. 3 but with rectilinear grid superimposed. 5, the smaller *S. quadricissus* matched to the larger. 6, the match with the modified grid superimposed. 7, the modified grid alone.

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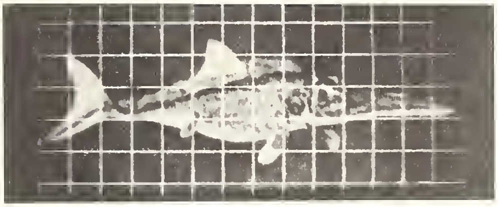
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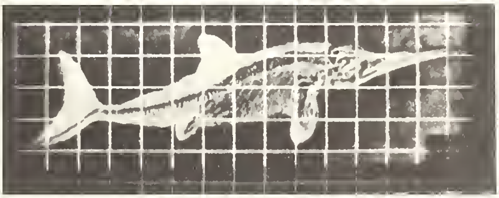
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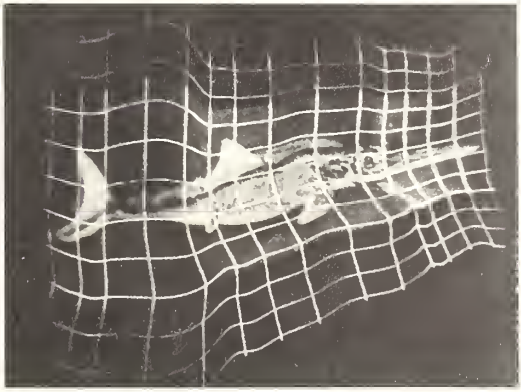
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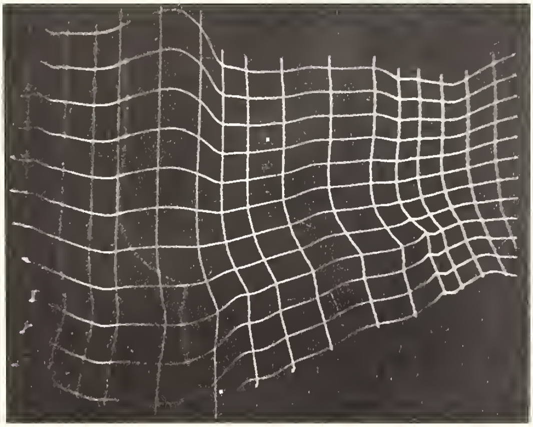
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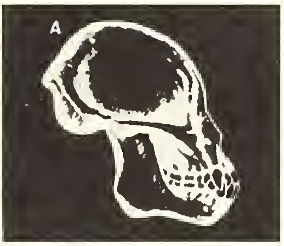
APPLEBY and JONES, *Stenopterygius*

of evolution in view of the large number of East and North African discoveries. However, the illustrations, taken from skulls and their reconstructions in Romer (1966), after Napier and le Gros Clark; Robinson; McGregor and Weinert, illustrate the method.

Proconsul (Pl. 90, figs. 1, 2) was matched to *Australopithecus* (Pl. 90, figs. 3, 4) to give the composite (Pl. 90, fig. 5) and the grid superimposed (Pl. 90, fig. 6). The grid alone is shown in Plate 90, fig. 7. As the modified grid shows, there is little difference in the shapes of the braincases except for a slight relative elongation from *Proconsul* to *Australopithecus*. Most of the differences lie in the orbital and nasal regions and in the regions of the jaw and dentition. *Australopithecus* matches very well to *Pithecanthropus* from Java (Pl. 90, figs. 8, 9). The match (Pl. 90, fig. 10) and the match and grid and match alone are shown in Plate 90, figs. 11, 12 respectively. The grid as a whole shows a general contraction in the vertical direction which is greater posteriorly than anteriorly but the greatest contraction anteriorly is from the region of the nasal opening to the supra-orbital ridges and slightly above. Posteriorly, the greatest contraction is vertically at the base of the skull. Between and above these two contractions the braincase is considerably expanded, particularly posteriorly, compared with that of *Australopithecus*. When the same procedure is carried out on *Pithecanthropus* from Java and Pekin (Pl. 90, fig. 8 and Pl. 91, fig. 1 respectively) the region of the grid which covers the matched skulls (Pl. 91, figs. 4, 5) is far more linear in all directions, confirming the extremely close apparent similarity between the two forms. There is some slight contraction of the braincase posteriorly in Pekin man and the lower jaw is somewhat contracted vertically. The roof of the skull shows a contraction which may well be a sexual difference. Going on to modify Pekin man so that it fits Neanderthal man (Pl. 91, figs. 6, 7) requires a somewhat different modification, as the grid superimposed on Pekin man shows (Pl. 91, figs. 9, 10). Here, apart from a slight upward tilt of the facial region compared with the braincase, the most linear part of the skull is in the temporal region. Apart from this, the braincase has contracted posteriorly while the facial region and posterior part of the lower jaw have expanded anterolaterally. Finally, modification of Neanderthal to Cro-Magnon man (Pl. 91, figs. 6, 11) shows a slight linear contraction in the facial and nasal regions (Pl. 91, figs. 13–15) and slight relative expansion in the orbital region, but the outstanding features are the further vertical contraction of the upper tooth row, the appearance of the chin emminence, and the much larger increase of the braincase as a whole. It is interesting that braincase expansion is greatest at the beginning and end of this series.

EXPLANATION OF PLATE 90

Figs. 1–12. Phylogenetic variation in relatively closely related hominoids. 1, *Proconsul*. 2, the same with rectilinear grid superimposed. 3, *Australopithecus*. 4, *Australopithecus* with rectilinear grid superimposed. 5, *Proconsul* matched to *Australopithecus*. 6, the match with the modified grid superimposed. 7, the modified grid alone. 8, *Pithecanthropus* from Java. 9, *Pithecanthropus* from Java with rectilinear grid superimposed. 10, *Australopithecus* matched to *Pithecanthropus* from Java. 11, *Australopithecus* matched to *Pithecanthropus* with the modified grid superimposed. 12, the modified grid alone.



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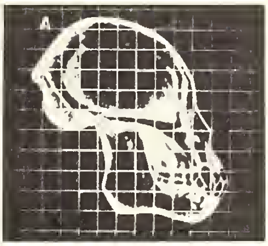

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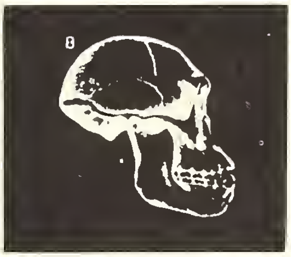

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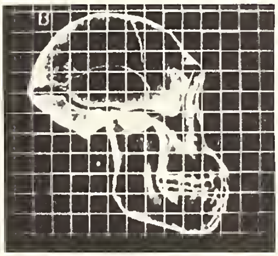

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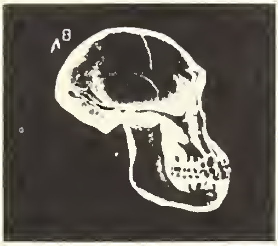

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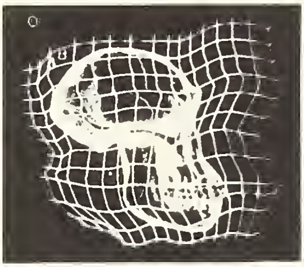

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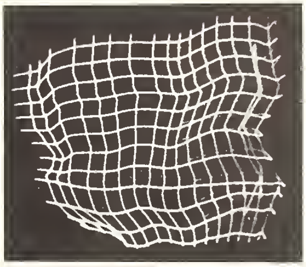
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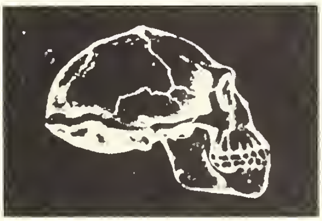
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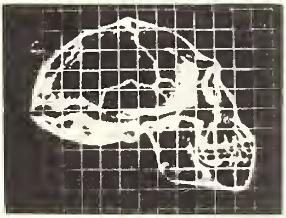
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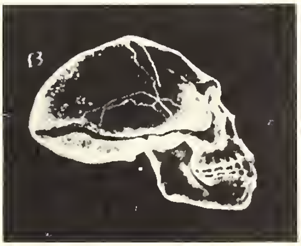

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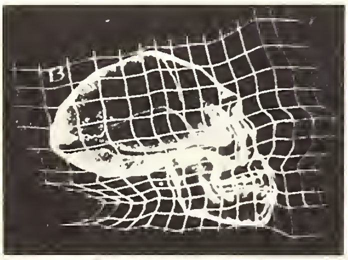

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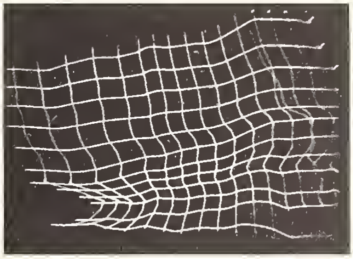
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APPLEBY and JONES, hominoid skulls

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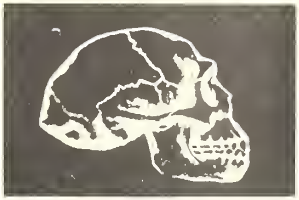
EXPLANATION OF PLATE 91

Figs. 1–15. Phylogenetic variation in relatively closely related hominoids (continued). 1, *Pithecanthropus* from Pekin. 2, the same with rectilinear grid superimposed. 3, *Pithecanthropus* from Java matched to *Pithecanthropus* from Pekin. 4, the match with modified grid superimposed. 5, the modified grid alone. 6, Neanderthal man. 7, Neanderthal man with rectilinear grid superimposed. 8, Pekin man matched to Neanderthal man. 9, Pekin man matched to Neanderthal man with the modified grid superimposed. 10, the modified grid alone. 11, Cro-Magnon man. 12, Cro-Magnon man with rectilinear grid superimposed. 13, Neanderthal man matched to Cro-Magnon man. 14, Neanderthal man matched to Cro-Magnon man with the modified grid superimposed. 15, the modified grid alone.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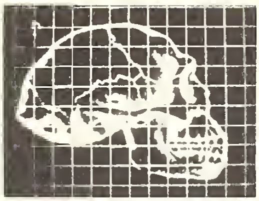
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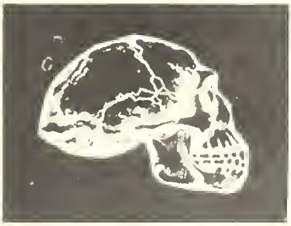
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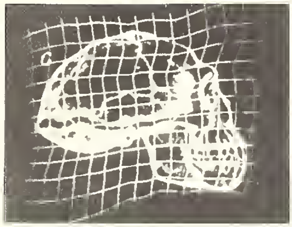
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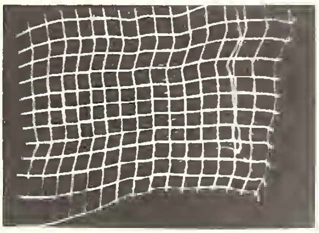
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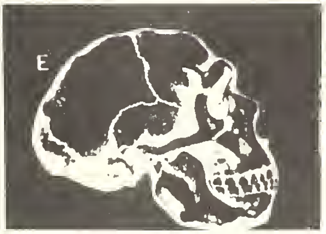

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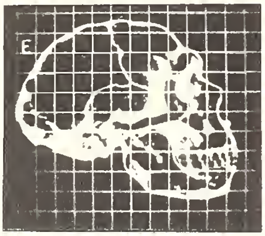

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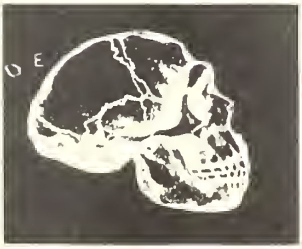

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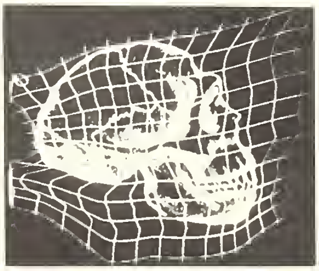
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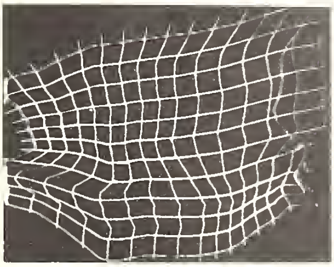
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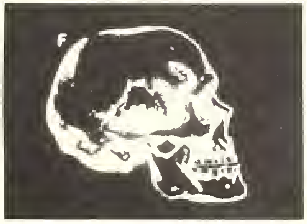

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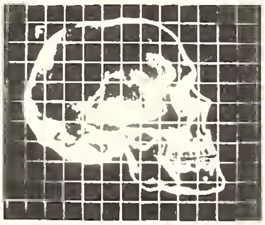

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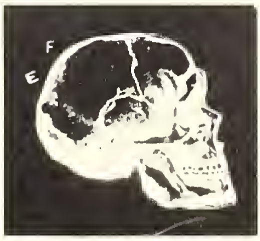

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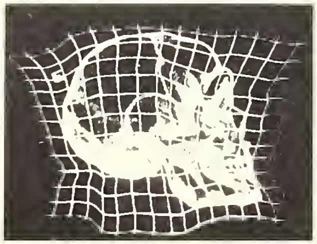
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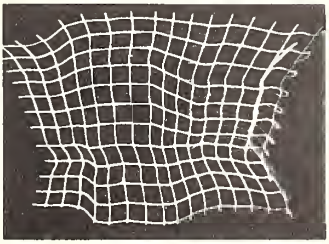
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SHORT COMMUNICATION

ILIOSUCHUS, A JURASSIC DINOSAUR FROM OXFORDSHIRE AND UTAH

by PETER M. GALTON

ABSTRACT. Ilia of the small theropod dinosaur *Iliosuchus incognitus* von Huene from the Stonesfield Slate (Middle Jurassic–Bathonian) of Oxfordshire are characterized by a prominent vertical ridge on the lateral surface. A similar ridge is present also on ilia of *Stokesosaurus clevelandi* Madsen from the Morrison Formation (Upper Jurassic–Tithonian) of Utah. This suggests that *Stokesosaurus* should be regarded as a junior synonym of *Iliosuchus*, and is further evidence of a land connection between Europe and North America during the Jurassic.

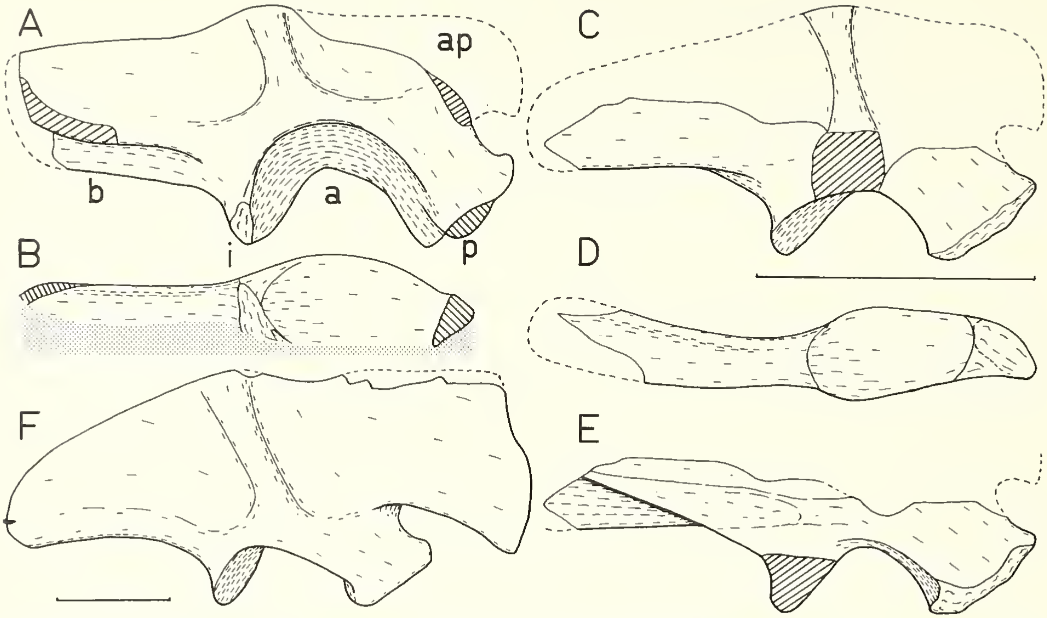
VON HUENE (1932) described a small and only partly prepared ilium from the Stonesfield Slate (Middle Jurassic–Bathonian) of Oxfordshire as a new genus and species of theropod dinosaur, *Iliosuchus incognitus*. The holotype was collected by G. W. Masson in 1880 from the *Gracilisphinctes progracilis* Zone of Stonesfield. *Iliosuchus* is listed by Romer (1966, p. 369) as a junior synonym of *Megalosaurus*; this is reasonable on the basis of the published figure (von Huene 1932, pl. 2, fig. 3) and in view of the fact that many bones of the large theropod *M. bucklandi* also are known from the Stonesfield Slate (Buckland 1824; von Huene 1926). However, preparation of the ilium (text-fig. 1A, B) shows that *Iliosuchus* is a distinct genus to which should also be referred another small Stonesfield ilium (text-fig. 1C–E) from Oxfordshire, originally figured as that of a young megalosaur by Phillips (1871, p. 212). These ilia are redescribed below and the relationships of *Iliosuchus* are considered. Institution names are abbreviated as follows: BM, British Museum (Natural History), London; OUM, Oxford University Museum; UUVP, University of Utah Vertebrate Paleontology Collection, Salt Lake City, U.S.A.

DESCRIPTION AND COMPARISONS

The most noticeable feature of the lateral surface of the holotype ilium of *I. incognitus* is the prominent vertical ridge which flares out anteriorly and posteriorly above the acetabular margin (text-fig. 1A). Anterior to this ridge, the bone is crushed and incomplete, so that the outline of the anterior process is unknown. As preserved, the maximum height is 42 mm, the maximum length is 89 mm, and the maximum width of the acetabulum is 32 mm. The other ilium (text-fig. 1C–E) is damaged and incomplete, but it is so like the holotype that, taking individual variation into account, it is reasonable to refer it to *I. incognitus*.

The lateral surface of the ilium of *M. bucklandi* (Stonesfield Slate, Oxfordshire) is smooth with no trace of a vertical ridge (Walker 1964, fig. 16*d*). The outline of the ilium of *Tyrannosaurus* (Upper Cretaceous, U.S.A.) is rather different, but there are traces of a vertical ridge (Romer 1923, fig. 1) which is interpreted by Russell (1972) as the boundary between the areas of origin of the anterior and posterior heads of the iliofemoralis muscle.

[Palaeontology, Vol. 19, Part 3, 1976, pp. 587–589.]



TEXT-FIG. 1. *Iliosuchus* ilia. A, B, *Iliosuchus incognitus* von Huene holotype BM R83, ×0·75, right ilium; A, lateral view; B, ventral view. C–E, *I. incognitus*, referred specimen OUM J29780, ×0·75, left ilium; C, lateral view printed in reverse; D, ventral view printed in reverse; E, medial view. F, *I. clevelandi* (Madsen) holotype UUVP 2938, ×0·30, left ilium in lateral view, printed in reverse after Madsen (1974, fig. 1A). a, acetabulum; ap, anterior process; b, brevis shelf; i, ischiadic head; p, pubic peduncle. Scale lines represent 5 cm.

The only other theropod ilium described to date that is similar to those of *Iliosuchus* is that of *Stokesosaurus clevelandi* Madsen, 1974 (text-fig. 1F) from the Brushy Basin Member of the Morrison Formation (Upper Jurassic–Tithonian) of the Cleveland-Lloyd Quarry in east central Utah. This ilium is larger (maximum length 220 mm, referred specimen 330 mm), and appears to be proportionally deeper with a large anterior process (text-fig. 1A, C, F). However, these differences are relatively minor. On the basis of the material described to date, *Stokesosaurus* Madsen, 1974 may therefore be regarded as a subjective junior synonym of *Iliosuchus* von Huene, 1932, and the name of the American species becomes *I. clevelandi* (Madsen). The systematic position of *Iliosuchus* is uncertain and therefore, although additional material may eventually prove that it belongs to the family Coeluridae, *Iliosuchus* is best regarded as a theropod *incertae sedis*.

The similarities between the dinosaurian faunas of the Morrison Formation of the western interior of North America and the Tendaguru Formation of Tanzania, East Africa can be accounted for only by assuming the presence of a land connection between these two areas some time during the Middle to Late Jurassic (Charig 1973; Colbert 1974; Cox 1974). Europe and North America also were presumably connected at this time, but faunal evidence for this is slight (Charig 1973; Cox 1974). The presence of *Iliosuchus* in both areas provides additional faunal evidence for a transatlantic connection during Middle to Late Jurassic times.

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Cover: *Calymene frontosa* Lindström, from Visby Beds (Silurian) of Gotland, Sweden.
Specimen Ar 27038 from Naturhistoriska Riksmuseet, Stockholm, photographed by
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THE DISTRIBUTION OF THE DINOFLAGELLATE *WETZELIELLA* IN THE PALAEOGENE OF NORTH-WESTERN EUROPE

by LUCY I. COSTA *and* CHARLES DOWNIE

ABSTRACT. The stratigraphical distribution of *Wetzeliella* in England, Belgium, and north Germany is reviewed. A very similar succession of species in these areas permits the establishment of eight *Wetzeliella* zones ranging from the late Upper Palaeocene to the Oligocene. Correlation based on *Wetzeliella* in north-west Europe is in agreement with that founded on calcareous nannoplankton. The zonation proposed for north-west Europe can be made to correspond with similarly based schemes established for the Upper Palaeocene–Lower Eocene of the southern Pyrénées (north-east Spain) and for the Palaeogene of the Alpine flysch (east France). In the Systematic Appendix, a new subgenus: *W.* (*Apectodinium*) and two new species: *W.* (*Apectodinium*) *paniculata* and *W.* (*W.*) *gochtii*, are introduced.

THE genus *Wetzeliella* Eisenack is one of the most characteristic and better-known elements in Palaeogene dinoflagellate assemblages. Since it was erected by Eisenack in 1938 this genus has received the attention of several investigators (Gocht 1955, 1967, 1969; Williams and Downie 1966; Wilson 1967; Vozzhennikova 1967), who considerably added to the knowledge on the morphology and taxonomy of the group. The relatively large number of works on Palaeogene microplankton assemblages published in the last decade has yielded abundant additional information on the distribution of many species in this genus. The stratigraphical range of *Wetzeliella* is relatively restricted: no species properly referable to this genus is known from sediments older than the Upper Palaeocene and it now seems certain that the genus becomes extinct in the Miocene. Of the thirty or so species of *Wetzeliella* described, the great majority occur in the Lower–Middle Eocene, the number decreases markedly towards the Oligocene and only one species (*W.* (*W.*) *symmetrica*) seems to occur in the Miocene. The picture offered by the group is that of a sudden and widespread first appearance in the late Upper Palaeocene, quickly followed by a rapid diversification which reached its maximum in the late Lower Eocene, and a progressive decline towards the Oligocene.

Wetzeliella has an extensive geographical distribution comprising eastern and western Europe, central Asia, New Zealand, Australia, and North America. Only one species has so far been recorded in South America and no records are known from Africa, the remainder of Asia, or the Antarctic. The most important centre of evolution and diversification for the genus appears to be western Europe, where the greatest number of species has been recorded. Australia and New Zealand appear to be other centres of evolution with endemic species, but the number of taxa and of published records is here much lower than in western Europe.

The first reference to the importance of *Wetzeliella* in Palaeogene biostratigraphy was made by Wilson (1967) who studied its distribution in the Palaeocene–Eocene of New Zealand. But it is only recently that the usefulness of members of this genus

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as stratigraphical indicators in Europe gained recognition. Russian workers have included *Wetzeliella* in the analysis of Eocene and Oligocene deposits in Ukraine, Crimea, and Tadjikistan (Grigorovich 1969, 1971; Grigorovich and Vyesyelov 1973; Olyenik 1973). Downie *et al.* (1971) proposed the '*Wetzeliella* phase' to characterize the Oldhaven and Woolwich Beds in south-east England and to apply this to correlation with the Belgian Landenian. The first zonal scheme based on *Wetzeliella* was introduced by Caro (1973) for the Upper Palaeocene–Lower Eocene of the southern Pyrénées in north-east Spain. In a work on the palynology, calcareous nannoplankton, and stratigraphy of the Alpine flysch in Haute Savoie (east France), Jan du Chêne *et al.* (1976, in press) also give special attention to the distribution of *Wetzeliella* in their zonation.

This paper is part of a more extensive reappraisal of the genus *Wetzeliella* in which the morphology, taxonomy, and evolution of this group have been reviewed. The establishment of a zonation scheme is based on an examination of the morphology and evolution in the different lineages distinguished within the genus, a detailed account of which will be presented in a separate paper. The systematics of *Wetzeliella* need some readjustments, the necessary changes are formalized in the Systematic Appendix at the end of this paper, this also includes a list of the taxa mentioned in the text.

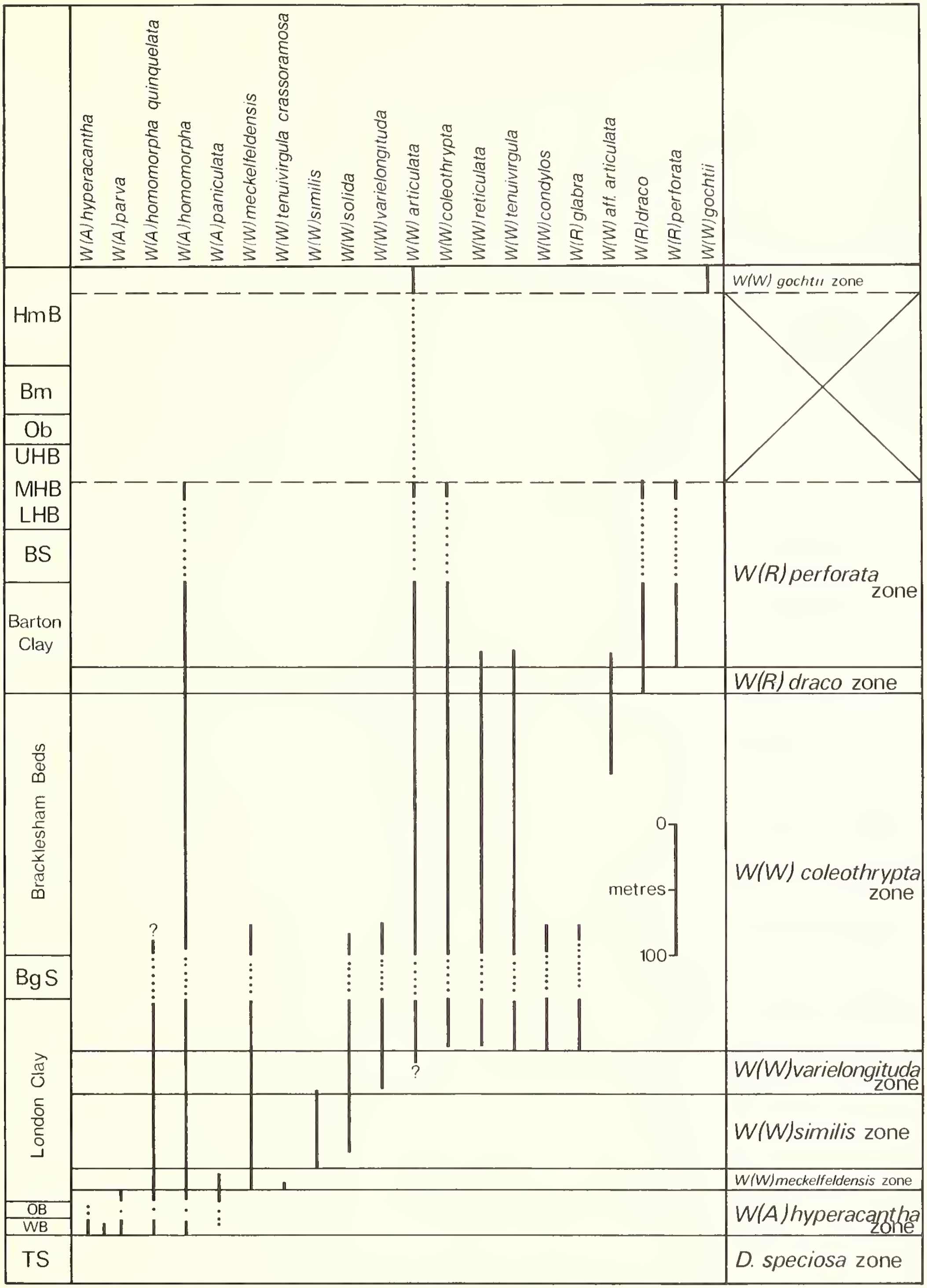
MATERIAL

The abundant British material employed for this work comprises several stratigraphical sequences ranging from the Upper Palaeocene to the Middle Oligocene, developed in the London and Hampshire basins, both in the south-east of England. The microplankton assemblages from these sections have already been studied by several workers (Williams, unpublished thesis, Sheffield 1963; Williams and Downie 1966; Husain, unpublished thesis, Sheffield 1967; Eaton 1971; Downie *et al.* 1971; Bujak, unpublished thesis, Sheffield 1973; Liengjarern, unpublished thesis, Sheffield 1973) and zonal schemes based on dinoflagellates have been proposed for the main sections.

A series of borehole samples from Meckelfeld (near Hamburg, north Germany) was made available by Professor E. Martini and Dr. P. Benedek (Frankfurt) who are currently studying the nannoplankton and microplankton content of the same. Dr. H. Gocht (Tübingen) made available material from his work on two Meckelfeld boreholes (1969); part of Eisenack's type material collection was also examined. Additionally, Dr. J. De Coninck (Gent) provided samples from the boreholes of Kallo, Merelbeke, and Sint Jan (Belgium). Photographs and valuable information about the species of *Wetzeliella* in the Alpine flysch were made available by Dr. R. Jan du Chêne (Geneva).

THE HISTORY OF *WETZELIELLA* IN SOUTH-EAST ENGLAND

The first occurrence of *Wetzeliella* in England is in the Woolwich Beds (Upper Palaeocene) (text-fig. 1) where there is a massive incoming of individuals belonging to the species *Wetzeliella* (*Apectodinium*) *homomorpha* subsp. *quinquelata*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *parva*, and *W.* (*A.*) *hyperacantha* (Pl. 92,



TEXT-FIG. 1. The range of selected *Wetzeliella* spp. in England. TS, Thanet Sands, WB, Woolwich Beds; OB, Oldhaven Beds; BgS, Bagshot Sands; BS, Barton Sands; LHB, Lower Headon Beds; MHB, Middle Headon Beds; UHB, Upper Headon Beds; Ob, Osborne Beds; Bm, Bembridge Marl; HmB, Hamstead Beds.

fig. 6), the first being, by far, the most abundant. The *Wetzeliella* species in the Woolwich Beds are closely interrelated, the discrimination between them often being difficult due to the continuous variation in the critical morphological characters and the abundance of intermediate forms. These taxa conform to a clearly distinct group within the genus and they are accorded here the status of a separate subgenus: *Wetzeliella* (*Apectodinium*). The species involved differ from other *Wetzeliella* species by lacking a clearly separate endoblast (the endophragm being closely appressed to the periphragm) and, consequently, a distinct pericoel. The association of *Wetzeliella* species in the Woolwich Beds constitute the '*Wetzeliella* phase' of Downie *et al.* (1971) and completely dominates the microplankton assemblages.

In the lower part of the London Clay, a new species, *W.* (*A.*) *paniculata* (Pl. 92, fig. 1) becomes quite abundant. Two species substantially different from those mentioned above, *W.* (*W.*) *meckelfeldensis* and *W.* (*W.*) *tenuivirgula* subsp. *crassoramosa* first occur a few metres above the base of the London Clay in both the London and the Hampshire basins. These species, with a subrhombic outline, four well-developed horns, and a well-differentiated and usually thick-walled endoblast, are easily distinguished from *W.* (*A.*) *homomorpha* and *W.* (*A.*) *paniculata* which also abound in these assemblages. Two taxa from the beds below, *W.* (*A.*) *parva* and *W.* (*A.*) *hyperacantha*, apparently disappear at this point. *W.* (*W.*) *similis*, a species presumably derived from *W.* (*W.*) *meckelfeldensis*, is first recorded in the London Clay a few metres above the first appearance of this latter. The appearance of *W.* (*W.*) *similis* at Whitecliff Bay (Isle of Wight) coincides with the planktonic foraminifera datum recognized by Wright (1972) in this section, this datum is marked by the incoming of a number of planktonic foraminifera species not recorded earlier. *W.* (*W.*) *solida*, originating from *W.* (*W.*) *similis*, appears shortly above this horizon and becomes progressively more abundant until it almost completely replaces *W.* (*W.*) *similis* in the assemblages. *W.* (*A.*) *paniculata* becomes very rare and disappears in this part of the section. *W.* (*A.*) *homomorpha* is still abundant, particularly at Alum Bay. *W.* (*W.*) *meckelfeldensis* is also present although it is rare. The next stage in the succession of species of *Wetzeliella* in the London Clay is marked by the appearance of *W.* (*W.*) *varielongituda*, probably derived from *W.* (*W.*) *solida* or *W.* (*W.*) *similis*, near the top of the London Clay at Whitecliff Bay and about 80 m above the base of the London Clay at Herne Bay. *W.* (*W.*) *solida*, *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *lunaris*, and *W.* (*A.*) *homomorpha* are also present in these assemblages.

A remarkable increase in the diversity of this genus is registered approximately 35 m below the top of the London Clay at Sheppey, with the incoming of a number of species such as *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *tenuivirgula*, *W.* (*W.*) *articulata*, *W.* (*W.*) *reticulata*, *W.* (*Rhombodinium*) *glabra*, and *W.* (*W.*) *condylos*. All the species occurring immediately below this horizon persist into these assemblages, although some of them (e.g. *W.* (*W.*) *solida* and *W.* (*W.*) *meckelfeldensis*) are very rare. *W.* (*A.*) *homomorpha homomorpha* is now dominant over the subspecies *quinquelata*. The only section of the London Clay where this assemblage is represented is that at Sheppey (Kent), but it also occurs at the bottom of the Bracklesham Beds in the Isle of Wight. The microplankton assemblages in the lowermost Bracklesham Beds (Bed I of the section at Whitecliff Bay, Fisher 1862) contain almost the same *Wetzeliella* species as those at the top of the London Clay at Sheppey, although in less abundance.

Above this bed, the number of species of *Wetzeliella* decreases considerably. *W.* (*R.*) *glabra*, *W.* (*W.*) *solida*, and *W.* (*W.*) *varielongituda* apparently do not occur above this bed; *W.* (*A.*) *homomorpha* subsp. *quinquelata* occurs only occasionally in the Bracklesham Beds, the subgenus being now represented almost exclusively by *W.* (*A.*) *homomorpha* subsp. *homomorpha* which is very abundant in some horizons of the section at Alum Bay. The diversity of *Wetzeliella* is further diminished above the beds with *Nummulites variolarius* and *N. laevigatus* (Fisher's Bed VIII) where *W.* (*W.*) *condylos* and *W.* (*W.*) *meckelfeldensis* seem to disappear. The composition of the assemblages in so far as *Wetzeliella* is concerned is very uniform in the remainder of the Bracklesham Beds and no new species of the genus appears in the sequence. *W.* (*W.*) *articulata* and *W.* (*W.*) *coleothrypta* occur throughout the Bracklesham Beds and may be very abundant in some horizons. Although the *Wetzeliella* assemblages vary very little throughout this sequence, considerable intraspecific variation is observed in *W.* (*W.*) *articulata* and also, although less pronounced, in *W.* (*W.*) *coleothrypta*. This variability seems to be, at least in part, due to environmental control and similar varieties may not occur elsewhere. However, a distinction of varieties of *W.* (*W.*) *articulata* may possibly prove a useful element to apply in correlation, at least within the Hampshire Basin. In the Upper Bracklesham Beds (Fisher's Beds XI–XIX) the forms listed here as *W.* (*W.*) aff. *articulata* (Pl. 92, fig. 4) become very abundant; similar forms are found in the Bournemouth Marine Beds and the Hengistbury Head Beds, as well as in the Lower Barton Clays.

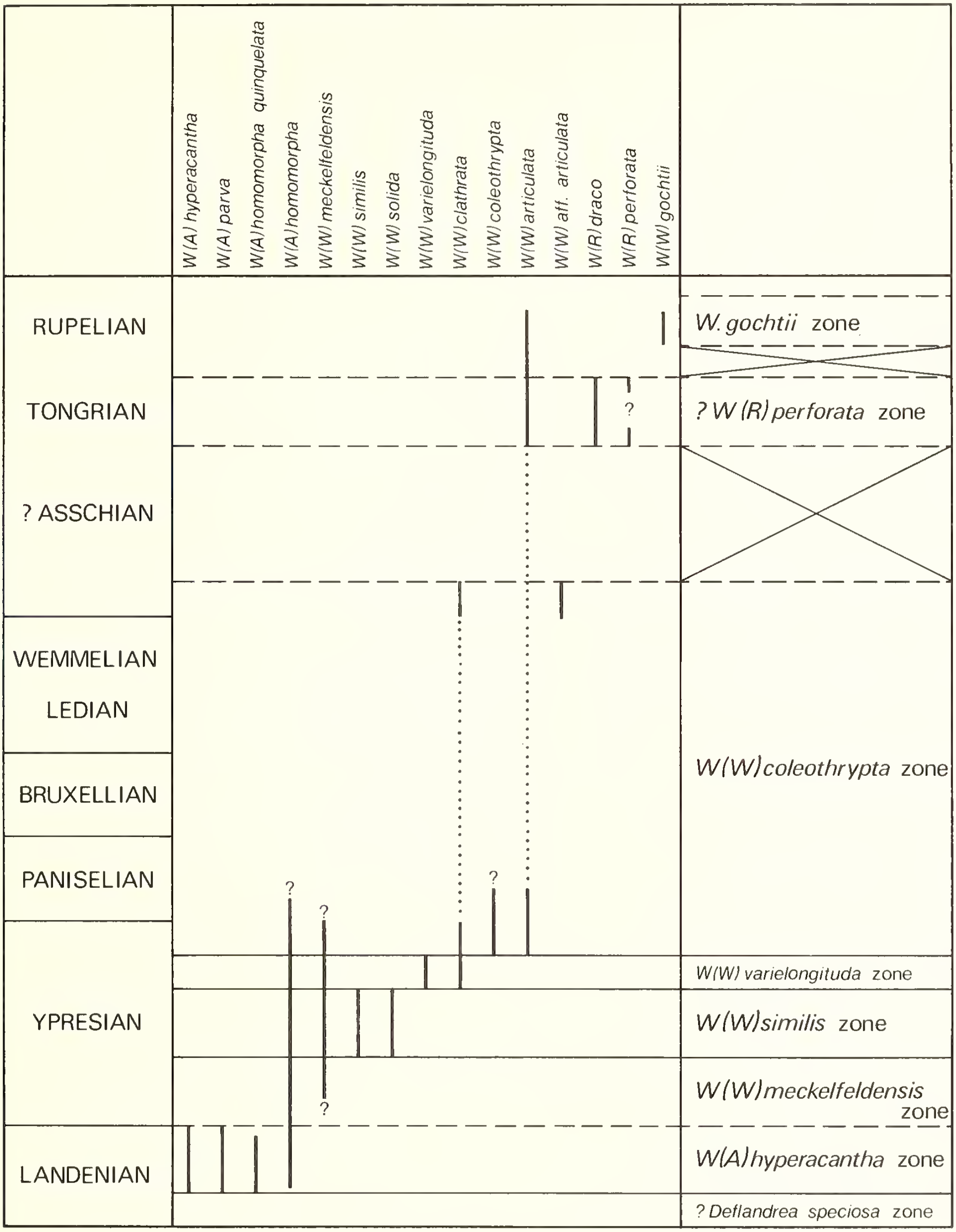
The base of the Barton Clays, marked by the *N. prestwichianus* Bed, registers the first appearance of *W.* (*R.*) *draco*, this species is, in fact, one of the very few elements in the microplankton assemblages that enables a distinction to be made between the top of the Bracklesham Bed (Fisher's Beds XVII–XIX), dinoflagellate zone 5 of Eaton, unpublished thesis, Sheffield 1969) and the base of the Barton Clays. The forms of *W.* (*R.*) *draco* in the Barton Clays are considerably smaller than the German type material for the species, but they are identical to this in all remaining characters. About 25 m above the base of the Barton Clays at Highcliffe, *W.* (*R.*) *perforata* (Pl. 92, fig. 5) is first recorded. This species presumably derives from *W.* (*R.*) *draco*, which it resembles in most characters (including size) and from which it is distinguished by the strongly perforated periphragm. Also in the Middle Barton Beds, an unpublished species of Bujak (thesis, Sheffield 1973) which is apparently related, if not synonymous, to *W.* (*W.*) *symmetrica* makes its first appearance, persisting up to the top of the Barton Clays. Apart from those already mentioned, other species recorded in this sequence are: *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *articulata*, *W.* (*W.*) *reticulata*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, and *W.* (*R.*) *longimanum*. The succession of *Wetzeliella* species is interrupted above the *Chama squamosa* Beds of the Bartonian, and the next records of the genus are found in the Middle Headon Beds with *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *articulata*, *W.* (*A.*) *homomorpha*, *W.* (*R.*) *draco*, *W.* (*R.*) *longimanum*, and *W.* (*R.*) *perforata*. The succession is again interrupted above these beds, dinoflagellates being very scarce, when not absent, in the overlying Upper Headon Beds, Osborne Beds, and Bembridge Beds, as well as in the Lower Hamstead Beds. The only species of *Wetzeliella* in the Upper Hamstead Beds are *W.* (*W.*) *articulata* and *W.* (*W.*) *gochtii* n. sp. (Pl. 92, figs. 2–3), which are the last representatives of the genus recorded in England.

THE DISTRIBUTION OF *WETZELIELLA* IN BELGIUM

De Coninck's works on the microplankton of the Belgian Ypresian (1965, 1968, 1972) enable a precise correlation between this and the Upper Palaeocene–Lower Eocene of south-east England. Only the distribution of *Wetzeliella* has been taken into account in the present work, but it appears most likely that a similar appraisal of the whole of the dinoflagellate assemblages in both areas would provide further support to the correlation proposed on text-fig. 4. Additional information on the distribution of *Wetzeliella* is provided by Rozen (1965), Morgenroth (1966), and Weyns (1970).

As can be seen on text-fig. 2, the succession of species of *Wetzeliella* in the sections studied by De Coninck is practically identical to that observed in the Woolwich Beds–London Clay–Lower Bracklesham Beds in south-east England (text-fig. 1). The typical assemblages of the Woolwich Beds are clearly identifiable in the Sables d'Ostende-ter-Streep (Landenian 2) which also lithologically resemble the Woolwich Beds. As *Wetzeliella* sp., De Coninck (1968, p. 21) includes *W.* (*A.*) *homomorpha homomorpha* (his pl. III, figs. 13–14, 17–18, 20), *W.* (*A.*) *h. quinquelata* (his pl. III, figs. 7–12, 15–16, 19) and, according to the description given by the author (p. 21), also *W.* (*A.*) *hyperacantha*. *W.* (*W.*) *meckelfeldensis* appears shortly above the base of the Argile d'Ypres (figured as *W.* aff. *symmetrica* in De Coninck 1968, pl. IV, fig. 9). As in the London Clay, *W.* (*W.*) *similis*, immediately followed by *W.* (*W.*) *solida*, appears a short distance above the first occurrence of *W.* (*W.*) *meckelfeldensis*, and *W.* (*W.*) *varielongituda* is first recorded about 70 m above the base of the Argile d'Ypres.

W. (*W.*) *coleothrypta* has not been recorded by De Coninck, but the species has now been found in a position corresponding to that in the London Clay at Sheppey. It should be pointed out that this species is easily confused with *W.* (*W.*) *clathrata*, to which it is very closely related, and it is sometimes difficult, particularly in unstained material, to tell one from the other. Also in the Upper Ypresian of Belgium, Morgenroth (1966) recorded *W.* (*R.*) *glabra*, as well as the species recorded by De Coninck. The Paniselian (P1) in the Kallo borehole appears to contain microplankton assemblages resembling those in the Lower Bracklesham Beds, including *W.* (*A.*) *homomorpha*, *W.* (*W.*) *articulata*, and *W.* (*W.*) *coleothrypta*. In the Argile d'Asse (Bartonian), Rozen (1965) recorded *W.* (*W.*) *clathrata* and *W.* (*W.*) *clathrata* subsp. *fasciata*, this latter appears to be, according to the illustrations, similar to *W.* (*W.*) aff. *articulata* recorded in the Upper Bracklesham Beds and Lower Barton Clays of south-east England. Weyns (1970) described the microplankton assemblages from the Sables de Grimmertingen (Tongrian) which include *W.* (*W.*) *articulata*, *W.* (*R.*) *draco*, and *W.* (*W.*) *varielongituda*. The specimen of *W.* (*R.*) *draco* figured by this author appears to have a perforated periphragm and could belong to *W.* (*R.*) *perforata*. The specimen figured as *W.* (*W.*) *varielongituda* does not correspond to this species and appears to belong to *W.* (*W.*) *symmetrica* or a related species. Two samples from the Rupel Clay were also available for the present work, they contain *W.* (*W.*) *articulata*, *W.* (*W.*) *ovalis*, *W.* (*W.*) *symmetrica*, and *W.* (*W.*) *gochtii* n. sp.



TEXT-FIG. 2. The range of selected *Wetzeliella* spp. in Belgium.

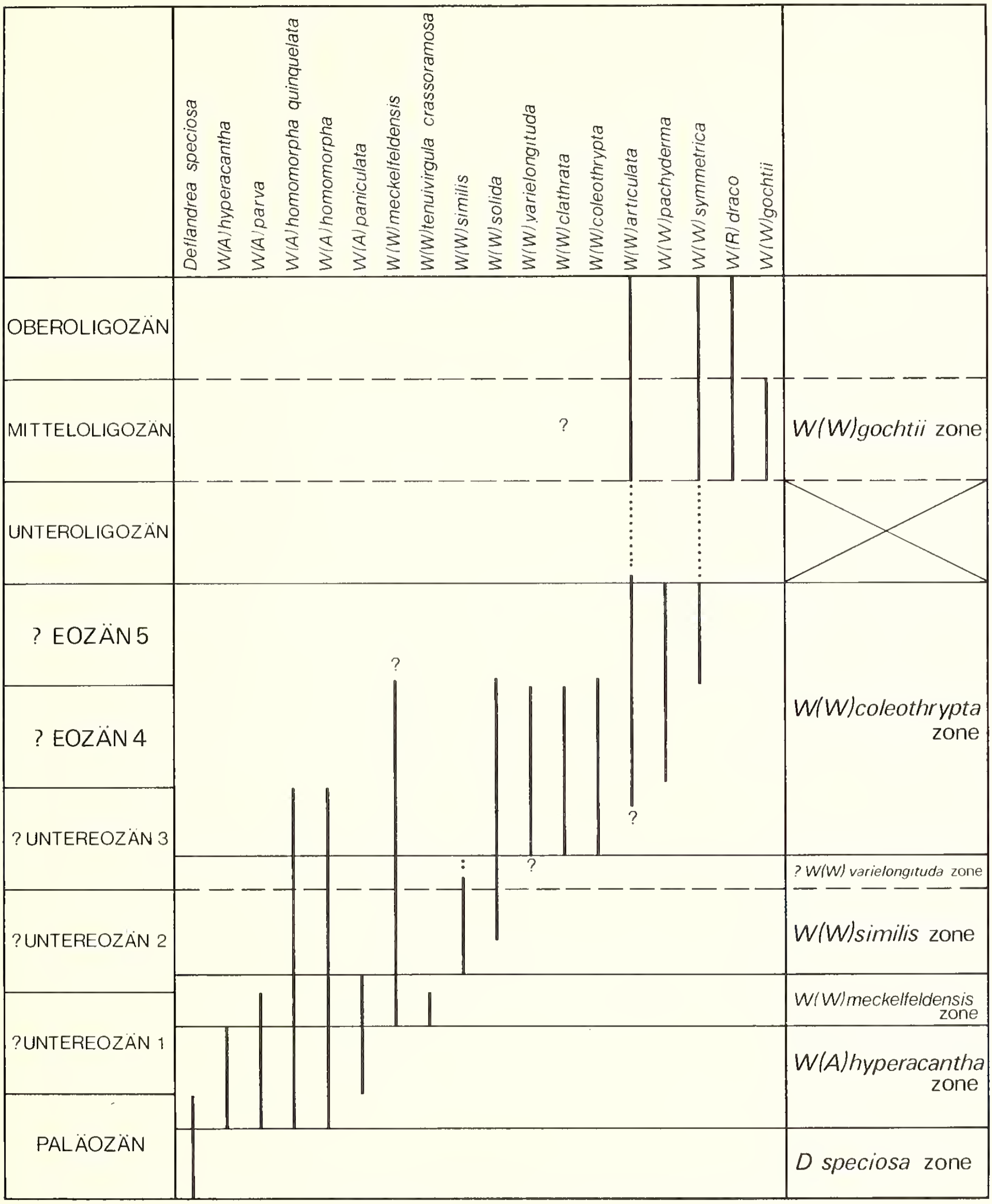
THE DISTRIBUTION OF *WETZELIELLA* IN NORTH GERMANY

The evidence provided by Morgenroth (1966), Agelopoulos (1967), and Gocht (1969), combined with the examination of the samples made available from Meckelfeld, give a fairly complete picture of the distribution of *Wetzeliella* in the Upper Palaeocene to Upper Eocene of north Germany. The information on the distribution of this genus in the Oligocene of north Germany has been taken from Eisenack (1938, 1954, 1965), Gocht (1955), Klumpp (1953), Weiler (1956), Maier (1959), Alberti (1961), Gerlach (1961), Brosius (1963), and Benedek (1972). Although the stratigraphical order of the Meckelfeld samples examined is known, their position relative to the German stages names is uncertain. These stages, however, have been established by Gocht (1969) in two borehole sections from the same locality. In constructing the table for text-fig. 3, an extrapolation has been made from these three sections. The scheme figured, consequently, should be regarded as provisional and the position of the stage boundaries may be modified as further information is made available.

The history of the genus *Wetzeliella* in north Germany appears to be, at least in general terms, the same as in the areas so far discussed. The succession of *Wetzeliella* species in the late Upper Palaeocene and Lower Eocene coincides with that observed in Belgium and south-east England. There are, however, some differences in the composition of the assemblages of the late Lower Eocene to Upper Eocene, part of which have already been pointed out by Morgenroth (1966). *W.* (*W.*) *coleothrypta* is rare or absent in assemblages corresponding to the Middle to Upper Eocene. *W.* (*R.*) *glabra*, which occurs both in England and in Belgium, is apparently absent in north Germany, where *W.* (*W.*) *samlandica* and *W.* (*W.*) *pachyderma*, not recorded in the areas treated above, are common. *W.* (*R.*) *draco* is apparently not present in the German stages attributed to the Upper Eocene, but the species is well known from Oligocene assemblages. *W.* (*R.*) *perforata* has not yet been recorded in north Germany. Oligocene dinoflagellate assemblages from north Germany include *W.* (*W.*) *articulata*, *W.* (*W.*) *ovalis*, *W.* (*W.*) *symmetrica*, *W.* (*W.*) *gochtii*, and *W.* (*R.*) *draco*. Maier (1959) has recorded *W.* (*W.*) *symmetrica* in deposits attributed to the Miocene.

WETZELIELLA ZONES IN NORTH-WEST EUROPE

The marked similarities observed in the distribution of *Wetzeliella* species in England, Belgium, and north Germany (area named here as north-west Europe), particularly in the late Upper Palaeocene and Lower Eocene, enables the genus to be applied to correlation and zonation within this area. A number of consecutive-range biozones based on first appearances of species of *Wetzeliella* can be distinguished, their position being apparently common to all areas under discussion. The succession of species in the Upper Eocene–Oligocene is not so clear. There are apparently some differences between England and Germany, such as the considerably earlier appearance of *W.* (*R.*) *draco* in the former and the absence of *W.* (*R.*) *perforata* in the latter. The evidence from Belgium is scant. Part of the differences observed may probably be due to stratigraphic gaps occurring in all three areas, and part also to gaps in the observation. Nevertheless, the evidence is enough to support the proposal of at least



TEXT-FIG. 3. The range of selected *Wetzeliella* spp. in north Germany.

a provisional scheme for the upper part of the Palaeogene, although the boundaries of the *Wetzeliella* zones have not been precisely determined. It should be noted that only the first occurrences of taxa have been taken into account in constructing the present scheme, as they are taken to be more reliable than the extinction of species. The disappearance of certain species may, however, be employed as additional features of the present zonation (e.g. the extinction of *W.* (*A.*) *hyperacantha* and *W.* (*A.*) *parva*, or the disappearance of a number of species in the Middle Eocene).

1. *Wetzeliella* (*Apectodinium*) *hyperacantha* Zone. Interval from the first appearance of the subgenus *Wetzeliella* (*Apectodinium*) to the first occurrence of *W.* (*Wetzeliella*) *meckelfeldensis*. Common *Wetzeliella* species: *W.* (*A.*) *parva*, *W.* (*A.*) *hyperacantha*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*, *W.* (*A.*) *paniculata*.

Distribution. England: Woolwich Beds at Charlton Brickpit, Erith and Upnor. Base of the London Clay at Whitecliff Bay and Herne Bay. Belgium: Sables d'Ostende-ter-Streep (Upper Landenian), Kallo. Germany: upper part of the Paläozän, Untereozän 1, Meckelfeld.

Remarks. Although *W.* (*A.*) *hyperacantha* is relatively rare in most of these assemblages, the name of the zone has been chosen to conform with the nomenclature introduced by Caro (1973).

2. *Wetzeliella* (*Wetzeliella*) *meckelfeldensis* Zone. Interval from the first occurrence of *W.* (*W.*) *meckelfeldensis* to the first appearance of *W.* (*W.*) *similis*. Common *Wetzeliella* species: *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *tenuivirgula* subsp. *crassoramosa*, *W.* (*A.*) *paniculata*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*.

Distribution. England: London Clay at Herne Bay (5–18 m above the base), Whitecliff Bay, Alum Bay, and Studland Bay. Belgium: Argile d'Ypres (377–357 m), Kallo. Germany: top of Untereozän 1, lower part of Untereozän 2, Meckelfeld.

3. *Wetzeliella* (*Wetzeliella*) *similis* Zone. Interval from the appearance of *W.* (*W.*) *similis* to the first occurrence of *W.* (*W.*) *varielongituda*. Common *Wetzeliella* species: *W.* (*W.*) *similis*, *W.* (*W.*) *solida*, *W.* (*W.*) *meckelfeldensis*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*.

Distribution. England: London Clay at Whitecliff Bay (41–71 m above the base), Alum Bay, and Herne Bay. Belgium: Argile d'Ypres (357–305 m), Kallo. Germany: part of the Untereozän 2, Meckelfeld.

4. *Wetzeliella* (*Wetzeliella*) *varielongituda* Zone. Interval from the first appearance of *W.* (*W.*) *varielongituda* to the appearance of *W.* (*W.*) *coleothrypta*. Common *Wetzeliella* species: *W.* (*W.*) *varielongituda*, *W.* (*W.*) *solida*, *W.* (*W.*) *lunaris*, *W.* (*W.*) *clathrata*, *W.* (*W.*) *edwardsi*, *W.* (*W.*) *meckelfeldensis*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*.

Distribution. England: London Clay at Allhallows (Kent) and at Whitecliff Bay. Belgium: Argile d'Ypres (305–266 m), Kallo. Germany: ?lower part of the Untereozän 3, Meckelfeld.

5. *Wetzeliella* (*Wetzeliella*) *coleothrypta* Zone. Interval from the first occurrence of *W.* (*W.*) *coleothrypta* to the first appearance of *W.* (*Rhombodinium*) *draco*. Common *Wetzeliella* species: *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *articulata*, *W.* (*W.*) *tenuivirgula*, *W.* (*W.*) *reticulata*, *W.* (*W.*) *clathrata*, *W.* (*W.*) *solida*, *W.* (*W.*) *varielongituda*, *W.* (*W.*) *condylos*, *W.* (*W.*) *pachyderma*, *W.* (*W.*) *samlandica*, *W.* (*R.*) *glabra*, *W.* (*W.*) *meckelfeldensis*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*, *W.* (*A.*) *homomorpha* subsp. *quinquelata*, *W.* (*W.*) aff. *articulata*.

Distribution. England: London Clay, 36 m below the top at Sheppey. Bracklesham Beds at Whitecliff Bay and Alum Bay. Bournemouth Marine Beds. Hengistbury Head Beds (below the *Nummulites prestwichianus* Bed). Belgium: Argile d'Ypres (above 266 m), Kallo; also at Sint Jan, Tielt, and Merelbeke. Paniselian (P1). Argile d'Asse. Germany: upper part of the Untereozän 3, Untereozän 4, and Eozän 5 (Oberes Eozän), Meckelfeld. Eozän 4 and Obereozän, Holstein.

Remarks. This extensive zone can be subdivided on two bases, the extinction of some *Wetzeliella* species and the range of varieties of *W.* (*W.*) *articulata*. A subzone is clearly defined in England at the top of the

Bracklesham Beds (Fisher's Beds XIV–XIX) by the occurrence of *W.* (*W.*) aff. *articulata*; this subzone appears to be also recognizable in the Argile d'Asse (Belgium), but not so in north Germany. The top of this zone has not been located in Germany, but it apparently corresponds to the top of the Eozän 5 (Oberes Eozän).

6. *Wetzeliella* (*Rhombodinium*) *draco* Zone. Interval from the appearance of *W.* (*R.*) *draco* to the appearance of *W.* (*R.*) *perforata*. Common *Wetzeliella* species: *W.* (*R.*) *draco*, *W.* (*W.*) *articulata*, *W.* (*W.*) aff. *articulata*, *W.* (*W.*) *coleothrypta*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*.

Distribution. England: Lower Barton Clays at Alum Bay (base to 36 m), Whitecliff Bay, Highcliffe. Hengistbury Head Beds (above the *Nummulites prestwichianus* Bed) at Hengistbury Head.

Remarks. This zone cannot be established either in Belgium or in Germany due, apparently, to the existence of stratigraphic discontinuities where the present zone should occur. *W.* (*R.*) *draco* is known to occur in the Upper Eocene of off-shore Atlantic Canada (Williams 1975) but in north Germany and Belgium it has only been recorded in the Oligocene.

7. *Wetzeliella* (*Rhombodinium*) *perforata* Zone. Interval from the first occurrence of *W.* (*R.*) *perforata* to the first appearance of *W.* (*W.*) *gochtii* n. sp. Common *Wetzeliella* species: *W.* (*R.*) *perforata*, *W.* (*R.*) *draco*, *W.* (*R.*) *longimanum*, *W.* (*W.*) *articulata*, *W.* (*W.*) *coleothrypta*, *W.* (*W.*) *symmetrica*, *W.* (*A.*) *homomorpha* subsp. *homomorpha*.

Distribution. England: the base of this zone lies 36 m above the base of the Barton Clays at Highcliffe; the upper part is represented by the Middle Headon Beds at Whitecliff Bay. Belgium: ?Sables de Grimmertingen (Tongrian).

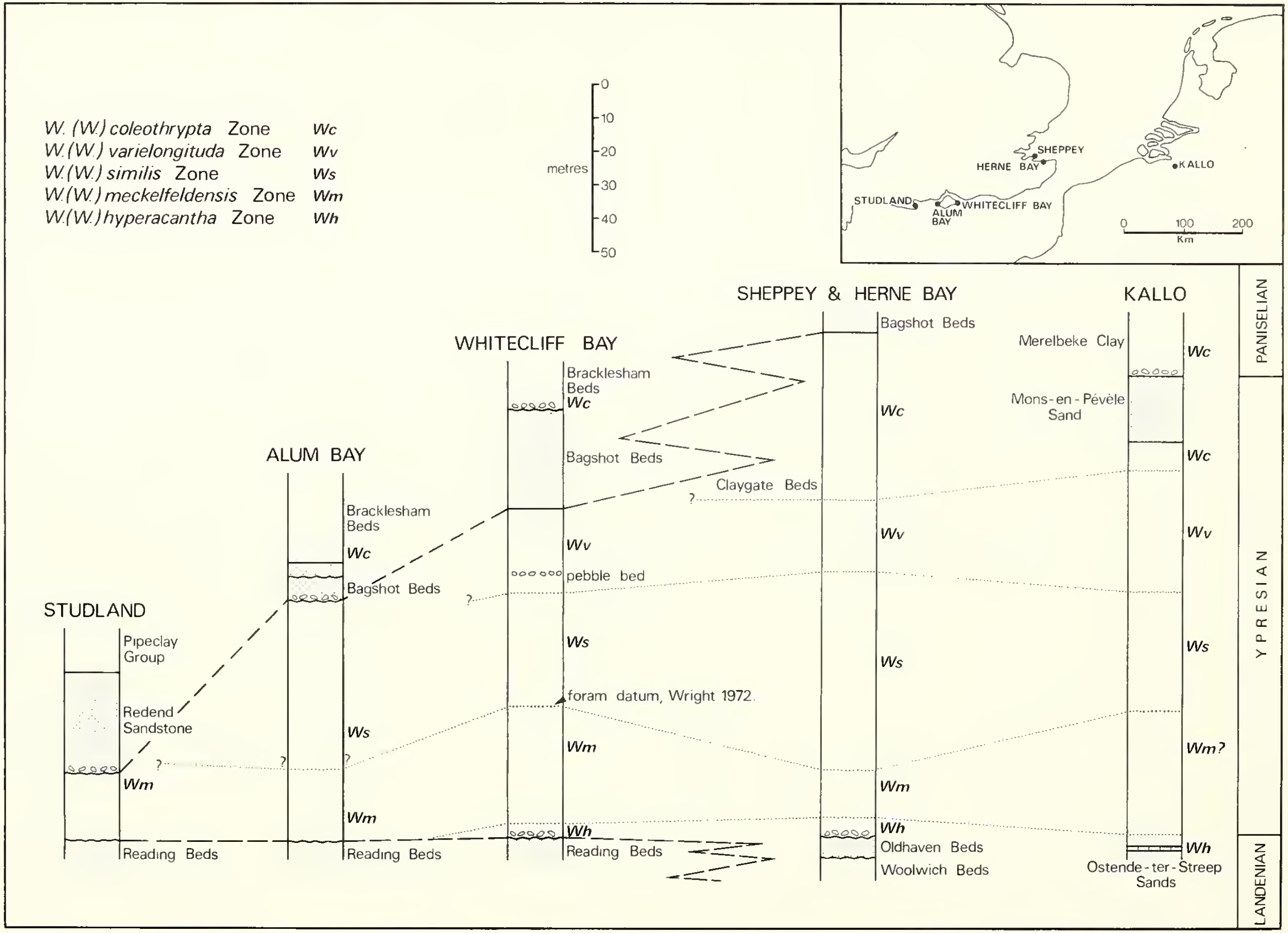
8. *Wetzeliella* (*Wetzeliella*) *gochtii* Zone. The base of this zone is at the first appearance of *W.* (*W.*) *gochtii*. Its position cannot be accurately established in the English succession because of unfavourable environments between the Middle Headon Beds and the Upper Hamstead Beds. The zone is recorded from the Upper Hamstead Beds of the Isle of Wight, from the Rupel Clay in Belgium, and from the Lintforten Schichten of Germany (Benedek 1972). Common *Wetzeliella* species: *W.* (*W.*) *gochtii*, *W.* (*W.*) *symmetrica*, *W.* (*W.*) *articulata*, *W.* (*W.*) *ovalis*, *W.* (*R.*) *draco*.

Remarks. This zone should be considered tentative until fuller examination of the Belgian and German sequences has been carried out.

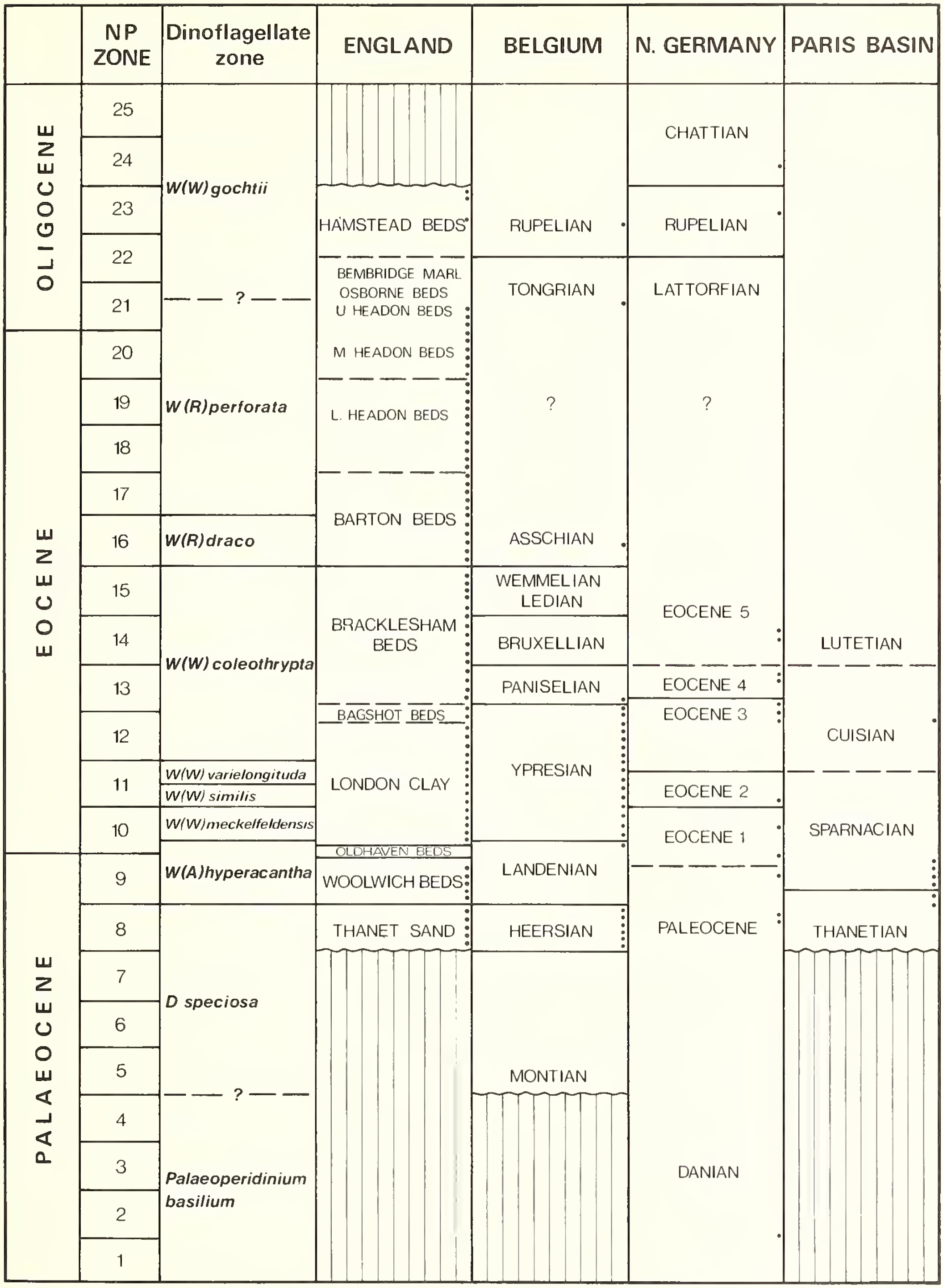
CORRELATION BASED ON *WETZELIELLA* IN NORTH-WEST EUROPE

The application of the zonation based on *Wetzeliella* can be extended from the western part of the Hampshire Basin to Belgium and north Germany and is particularly effective in the Upper Palaeocene and Lower Eocene.

The first appearance of *Wetzeliella* is a valuable datum recognizable in several European localities in and outside the present area. The *W.* (*A.*) *hyperacantha* Zone allows correlation of the Woolwich Beds with the Landenian, the Lower Sparnacian, and the upper part of the German Paläozän (text-fig. 5). The top of the *W.* (*A.*) *hyperacantha* Zone lies in the basal few metres of the London Clay at Herne Bay and Whitecliff Bay. The top of this zone has not been located at Alum Bay, but it may lie at the base of the London Clay. De Coninck (1968) shows the incoming of *W.* (*W.*) *meckelfeldensis* 2·85 m above the base of the Argile D'Ypres and the occurrence of *W.* (*A.*) *parva* up to this point; in his later work (1972) the main change is indicated at the base of the clay and *W.* (*A.*) *parva* restricted to the Landenian. The top of the present zone therefore either coincides with the Landenian/Ypresian boundary or lies about 3 m higher. In any case, the London/Ypres Clay transgression appears to be very rapid, if not simultaneous, over the whole area, only a slight overlap is



TEXT-FIG. 4. Correlation of the London Clay and Argile d'Ypres based on *Wetzeliella* spp. Dashed lines, lithological boundaries; dotted lines, palaeontological boundaries.



	NP ZONE	Dinoflagellate zone	ENGLAND	BELGIUM	N. GERMANY	PARIS BASIN
OLIGOCENE	25	W(W)gochtii		RUPELIAN	CHATTIAN	
	24					
	23		HAMSTEAD BEDS		RUPELIAN	
	22					
	21	?	BEMBRIDGE MARL OSBORNE BEDS U HEADON BEDS	TONGRIAN	LATTORFIAN	
EOCENE	20	W(R)perforata	M HEADON BEDS	?	?	
	19		L. HEADON BEDS			
	18					
	17		BARTON BEDS	ASSCHIAN	EOCENE 5	
	16	W(R)draco				
	15	W(W) coleothrypta	BRACKLESHAM BEDS	WEMMELIAN LEDIAN		
	14			BRUXELLIAN		LUTETIAN
	13			PANISELIAN	EOCENE 4	CUISIAN
	12		BAGSHOT BEDS	YPRESIAN	EOCENE 3	
	11	W(W) varielongituda W(W) similis	LONDON CLAY		EOCENE 2	SPARNACIAN
	10	W(W)meckelfeldensis	OLDHAVEN BEDS		EOCENE 1	
PALAEOCENE	9	W(A)hyperacantha	WOOLWICH BEDS	LANDENIAN	PALEOCENE	THANETIAN
	8	D speciosa	THANET SAND	HEERSIAN		
	7			MONTIAN	DANIAN	
	6					
	5	?				
	4	Palaeoperidinium basilium				
	3					
	2					
	1					

TEXT-FIG. 5. General correlation in north-west Europe based on nannoplankton and dinoflagellates. Dots indicate approximate position of dinoflagellate assemblages.

possible on the west of the Hampshire Basin. The top of this zone in north Germany lies in the Eozän 1, presumably near the top of this stage. This zone can also be extended to the Paris Basin, where it occurs in the Sables de Bracheux (Thanetian II, Zone 1 of Chateauneuf and Gruas-Cavagnetto 1968). The *W.* (*A.*) *hyperacantha* Zone has also been widely recognized in the North Sea Basin.

The *W.* (*W.*) *meckelfeldensis* Zone appears to be 15-30 m thick in the London/Ypres Clay Basin. In the London Clay, its top coincides with the boundary between lower and upper dinoflagellate assemblages recognized by Williams (1963) and also with the position of the planktonic foraminifera datum of Wright (1972) at Whitecliff Bay. At Studland, the zone was recognized in a sample from within 2 m below the top of the London Clay. A considerable non-sequence is therefore present at Studland Bay which diminishes eastwards. At Alum Bay its position is uncertain because of the absence of critical species but this non-sequence most likely lies above the *W.* (*W.*) *similis* Zone. At Whitecliff Bay, the sands appear below the *W.* (*W.*) *coleothrypta* Zone while at Sheppey about 35 m of clay belonging to the *W.* (*W.*) *coleothrypta* Zone intervene before the onset of the Bagshot Sands. Thus, the regression appears to have started at about the beginning of the *W.* (*W.*) *coleothrypta* Zone, and this was accompanied by uplift and erosion to the west. The Mons-en-Pévèle Sands, near the base of the *W.* (*W.*) *coleothrypta* Zone in Belgium, appear to be somewhat younger than the Bagshot Sands. The Mons-en-Pévèle Sands differ from the Bagshot Sands in their being marine in character, glauconitic and with abundant dinoflagellates, coccoliths, and foraminifera, and they presumably have a source to the east, in contrast to the barren (?fluvial) Bagshot Sands with a source to the west and northwest.

The *W.* (*W.*) *varielongituda* Zone is 25-45 m thick in the London/Ypres Clay Basin, its top is found about 35 m below the Bagshot Sands in the section exposed at Sheppey and a short distance below the Mons-en-Pévèle Sands at Kallo. This zone has not been clearly identified in north Germany; although *W.* (*W.*) *varielongituda* is abundant in some horizons, it is already associated with *W.* (*W.*) *coleothrypta* and presumably the *W.* (*W.*) *varielongituda* Zone should lie below these horizons, probably in the lower part of the Untereozän 3.

The *W.* (*W.*) *coleothrypta* Zone extends through a thick succession including not only the upper 35 m or so of the London Clay at Sheppey but also the whole of the Bracklesham Beds. This zone embraces the calcareous nannoplankton zones 12-15 of Martini (1971) and covers a number of dinoflagellate zones established by Eaton (1971) for the Bracklesham Beds. The present zone is recognizable in the uppermost few metres of the Argile d'Ypres, the Mons-en-Pévèle Sands, and the Merelbeke Clay. It is also found in the Eozän 3, 4, and 5 of Germany. The Røsnaes Clay of Denmark (Caro 1973; Caro *et al.* 1975) may either belong to this zone or lie as early as the *W.* (*W.*) *similis* Zone. The position is not clear from the available information, but the occurrence of *W.* (*W.*) *pachyderma* (present also in the Untereozän 4 and Eozän 5 of north Germany) and *W.* (*W.*) *clathrata* suggests the presence of the *W.* (*W.*) *coleothrypta* Zone.

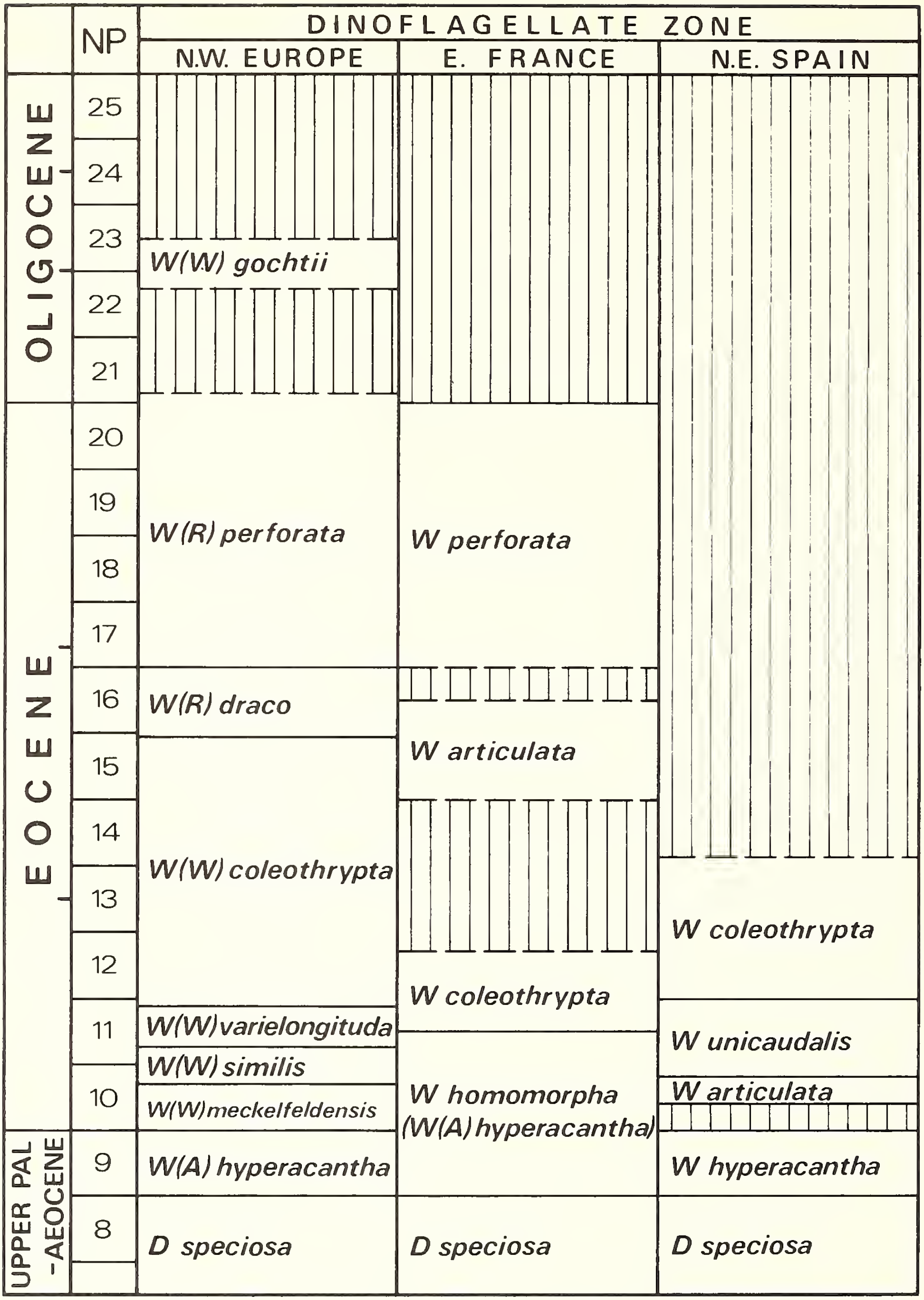
The *W.* (*R.*) *draco* Zone occupies only the lower part of the Barton Clay, its base being located immediately above the *Nummulites prestwichianus* Bed. This zone has not been recognized outside England, although the Argile d'Asse in Belgium might be its equivalent. The *W.* (*R.*) *perforata* Zone begins in the Middle Barton Clay and extends up to the top of this sequence; it has also been recognized in the Middle Headon Beds. The Sables de Grimmertingen (Tongrian) which contain forms resembling *W.* (*R.*) *perforata* may belong to this zone. The *W.* (*R.*) *perforata* Zone has not been recognized in north Germany.

The highest zone, that of *W.* (*W.*) *gochtii*, is found in the Upper Hamstead Beds. The base of this zone has not been located since the intervening Upper Headon Beds, Osborne Beds, Bembridge Beds, and Lower Hamstead Beds are for the most part non-marine (Liengjarern, unpublished thesis, Sheffield 1973) and contain very few dinoflagellates. The *W.* (*W.*) *gochtii* Zone occurs in the Argile de Rupel in Belgium and also in the Lintforter Schichten (Rupelian) of Tönisberg in north Germany. Above the Middle Oligocene in western Europe, *Wetzeliella* is restricted to very few species (*W.* (*W.*) *symmetrica*, *W.* (*W.*) *articulata*, and *W.* (*R.*) *draco*) and the genus appears to be of little value in correlation.

WETZELIELLA IN OTHER WEST EUROPEAN AREAS

So far the discussion has been restricted to the distribution and stratigraphic application of *Wetzeliella* in north-west Europe (south-east England, Belgium, and north Germany), but a large number of the *Wetzeliella* species present in this area are also well known from other European localities. As mentioned earlier, *Wetzeliella* has already been employed in the construction of biostratigraphical schemes in the Palaeocene–Lower Eocene of the southern Pyrénées in north-east Spain (Caro 1973; Caro *et al.* 1975), the Alpine flysch in east France (Jan du Chêne *et al.* 1975) as well as in the Palaeogene of the Ukraine and Crimea (Grigorovich 1969, 1971). There are also a number of records from the Palaeocene–Eocene of France (Chateauneuf and Gruas-Cavagnetto 1968; Gruas-Cavagnetto 1968, 1970), the Priabonian of north Italy (Gruas-Cavagnetto 1974), the Eocene of Romania (Baltes 1969), and several deposits in the U.S.S.R. (Eisenack 1938, 1954; Alberti 1961; Vozzhennikova 1967; Olyenik 1973; Aristova 1973; Grigorovich and Vyesyelov 1973).

As shown on text-fig. 5, a correspondence can be established between the *Wetzeliella* zones in north-west Europe and Martini's standard zonation based on calcareous nannoplankton (1971), and correlation based on *Wetzeliella* agrees with that founded on calcareous nannoplankton. This provides a reliable stratigraphic reference that can be applied to correlate the *Wetzeliella* zones recognized for north-west Europe with those defined for the southern Pyrénées and the French Alps (text-fig. 6). The lowest dinoflagellate zone on text-fig. 6, the *Deflandrea speciosa* Zone, has been recognized (although its range is not established precisely) in England, Belgium, and north Germany immediately below the first occurrence of *Wetzeliella*. The *W.* (*A.*) *hyperacantha* Zone is common to all areas under consideration, its base, which in fact marks the beginning of the known history of *Wetzeliella*, can be regarded as an important stratigraphic datum which can be identified not only in the areas shown on text-fig. 6, but also in Greenland, the North Sea Basin, north France, and the U.S.S.R. and possibly also as far as Australia and New Zealand. The north-west European *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *similis*, and *W.* (*W.*) *varielongituda* zones have not been identified in other European areas, and there is no information



TEXT-FIG. 6. Comparison of the *Wetzeliella* zonal scheme for north-west Europe with those for the Pyrénées and the western Alps.

available about the distribution of the key species in deposits outside north-west Europe, although these species are known to occur in other localities. In zoning the section at Campo (southern Pyrénées), Caro (1973) leaves a gap in the scheme above the top of the *W.* (*A.*) *hyperacantha* Zone, this may be the equivalent of part of the missing boreal zones. Caro's *W. articulata* Zone corresponds to the nannoplankton zone NP 10. Typical *W.* (*W.*) *articulata*, however, does not seem to appear in north-west Europe at least until the NP Zone 11. Some possible precursors of this species, some of which were classified as *W.* (*W.*) *lunaris* by Gocht (1969), do occur as early as the *W.* (*W.*) *similis* Zone. The *W. unicaudalis* Zone of north-east Spain probably is the equivalent of the boreal *W.* (*W.*) *varielongituda* Zone and part of the *W.* (*W.*) *coleothrypta* Zone; *W. unicaudalis* has so far only been recorded in its type locality and no similar forms have been observed in north-west Europe. Caro's *W. coleothrypta* Zone, at the top of the section at Campo, most likely corresponds to the lower part of the zone established in north-west Europe on the same species.

In the Grés de Voirons (Alpine flysch), *W.* (*A.*) *hyperacantha* occurs in the lower part of the *W. homomorpha* Association established by Jan du Chêne *et al.* (1975), this part of the section corresponds to the *W.* (*A.*) *hyperacantha* Zone recognizable in all other areas. The *W. homomorpha* Association in the Alpine flysch extends up to the appearance of *W.* (*W.*) *coleothrypta* (in the NP Zone 11), i.e. it is equivalent to the north-west European *W.* (*W.*) *meckelfeldensis*, *W.* (*W.*) *similis*, and *W.* (*W.*) *varielongituda* zones. It should be noted that in some more northerly Lower Eocene sections, such as the London Clay at Alum Bay, neither the *W.* (*W.*) *similis* Zone nor the *W.* (*W.*) *varielongituda* Zone have been precisely established due to the fact that in most beds throughout the section the only species of *Wetzeliella* present is *W.* (*A.*) *homomorpha*. It appears that *W.* (*A.*) *homomorpha* favours environments in which other *Wetzeliella* species are rare or do not occur at all, in the case of the London Clay at Alum Bay possibly because of lower salinities in a near-shore environment as suggested by Downie *et al.* (1971). The absence of the critical *Wetzeliella* species in the Alpine flysch might also be due to environmental conditions. The *W.* (*W.*) *coleothrypta* Zone has also been established in the Grés de Voirons, its base is apparently contemporaneous with the base of the zone in north-west Europe, according to the nannoplankton zonal scheme. The top of this zone in the flysch is unknown since the section is interrupted by a stratigraphical discontinuity.

The next zone defined in the Alpine flysch is the *W. articulata* Association, of which neither the base nor the top have been established because of stratigraphical gaps. This zone, defined by Jan du Chêne *et al.* (1975) as equivalent to the NP Zone 15 or older, apparently corresponds to the upper part of the *W.* (*W.*) *coleothrypta* Zone in north-west Europe. The *W. perforata* Association of Jan du Chêne *et al.* ranges from the NP Zone 16 to the top of the NP Zone 20, which agrees with the distribution of the zone based on the same species in the south-east of England. *W.* (*R.*) *draco*, which in England appears below the *W.* (*R.*) *perforata* Zone apparently does not occur in the Alpine flysch until the Oligocene (Jan du Chêne, pers. comm.).

SYSTEMATIC PALAEONTOLOGY

Division PYRRHOPHYTA
Class DINOPHYCEAE Fritsch, 1935
Order PERIDINIALES Haeckel, 1894
Family DEFLANDREACEAE Eisenack, 1954, emend. Sarjeant and Downie 1974
Genus *Wetzeliella* Eisenack, 1938, emend. Williams and Downie 1966
Subgenus *Wetzeliella* (*Apectodinium*) subgen. nov.

Derivation of name. Greek, 'apektos', uncombed.

Type species. *Wetzeliella* (*Apectodinium*) *homomorpha* Deflandre and Cookson 1955; p. 254, pl. 5, fig. 7.

Diagnosis. A subgenus of the genus *Wetzeliella* with pericoel absent or confined to small areas at the base of the horns. At the archeopyle margins the periphragm and endophragm are in close contact when both walls are observable. The processes are randomly distributed over the test surface or some can be roughly arranged along part of sutural lines.

Remarks. The species in this subgenus are in general considerably smaller in size than the other *Wetzeliella* species. The endophragm, which may be absent, is very thin, usually difficult to observe, and in close contact with the periphragm over most of the surface, separating only, if at all, at the base of the horns. Deformations of the endophragm which do not affect the periphragm are observable in many specimens showing that the walls are, in fact, separate. However, in contrast to what occurs in other *Wetzeliella* subgenera, the two layers remain attached in the opercula and around the apertures of the archeopyle, so that the shape of the aperture is the same on both the periphragm and the endophragm.

The species in this subgenus are distinguished by the shape and size of the horns, but there are abundant intermediate forms between them so that specific determinations may be on occasions somewhat arbitrary.

The subgenus *Wetzeliella* (*Apectodinium*) resembles *Spinidinium* and some spinose species of *Deflandrea* (e.g. *D. echinoidea*, *D. macmurdoensis*, etc.) in the size, structure of the walls, absence of lateral horns in many forms, shape of the archeopyle, and distribution of the ornament, but it differs in the shape of the ornament. In *Spinidinium*, and similarly ornamented species of *Deflandrea*, the ornament consists of short rods or spines, solid or hollow and closed distally; on the other hand, *Wetzeliella* (*Apectodinium*) bears long hollow processes, simple or bifurcate, and usually open distally. This subgenus is taken to represent or be related to the original stock from which most other *Wetzeliella* species derived; its main characters, i.e. small size, poorly differentiated endoblast, absence of lateral horns in many forms, variability in the development of the horns, abundant processes randomly arranged or crudely in part along sutures, etc., are regarded as primitive for the genus *Wetzeliella*.

Wetzeliella (*Apectodinium*) *paniculata* sp. nov.

Plate 92, fig. 1

?1969 *Wetzeliella* sp. 1; Gocht; p. 21, pl. 10, fig. 8; text-fig. 14.
1973 *Wetzeliella* sp.; Caro; p. 368, pl. 5, fig. 3.

Derivation of name. Latin, 'paniculus', small tuft.

Diagnosis. A species of *Wetzeliella* (*Apectodinium*) with a broadly rounded to subtriangular epitract and a subpolygonal hypotract. Apical horn absent or very much reduced; lateral horns broad and commonly long; well-developed antapical horns with a broad proximal part usually projecting into a long and complexly branched process.

Type locality. London Clay (Lower Eocene), Alum Bay, Isle of Wight, England.

Holotype. R. 36/4, slide ML 1193, rep. Micropalaeontology Laboratory, Department of Geology, University of Sheffield.

Dimensions. Holotype: over-all tract length 81 μ, breadth 92 μ; endoblast length 66 μ, breadth 74 μ; apical horn 3 μ; lateral horns 15 μ; antapical horn right 17 μ, left 15 μ; processes length 5–17 μ. Observed range: over-all length 93–76 μ, breadth 95–76 μ; apical horn 0–4 μ; lateral horns 9–18 μ; antapical horns 11–20 μ; processes length 5–18 μ. Number of specimens measured: ten.

Description. The apical horn is absent or, if present, reduced to a short, blunt projection surmounted by a tuft of processes; the epitract is broadly rounded to subtriangular in outline. The lateral horns are variable in length and they may be reduced, but they are typically long, rather broad, sometimes bifurcating distally, and abundantly covered by processes. The antapical horns consist of a broad and usually short proximal part and a long, branched distal process; the proximal part of the antapical horns may be very short, the horns then being reduced to the long ramified process. Both antapical horns are of roughly the same length. The endophragm, which may be absent in some specimens, is frequently very thin and difficult to observe. The processes are long, intratabular, with sometimes tapering bases and long tubiform distal parts which may be simple, bifurcate or, at the antapical horns, complexly branched. The processes are commonly open distally, the distal margin bearing a variable number of very short aculei, but they may also be closed with simple or bifid distal endings. The archeopyle is of the type common to the subgenus, i.e. small, subquadrangular, with periphragm and endophragm in close contact at the margins.

Remarks. The present species resembles *W.* (*A.*) *homomorpha* subsp. *quinquelata*, from which it differs by the long lateral horns; there are, however, numerous transitional forms between these taxa. *W.* (*A.*) *paniculata* differs from *W.* (*A.*) *hyperacantha* mainly in the absence of a well-developed apical horn and in the shape of the antapical horns; these in *W.* (*A.*) *hyperacantha* are shorter and do not bear a long ramified process distally. Other species in the subgenus *Wetzeliella* (*Apectodinium*) are: *W. parva* Alberti, 1961, *Palaeontographica*, **A 116,** p. 8, pl. 1, figs. 14–18; *W. hyperacantha* Cookson and Eisenack, 1965, *Proc. Roy. Soc. Victoria*, **79,** pp. 134–135, pl. 16, figs. 3–6.

Subgenus *Wetzeliella* (*Wetzeliella*) Eisenack, 1938,
emend. Williams and Downie 1966
Wetzeliella (*Wetzeliella*) *gochtii* sp. nov.

Plate 92, figs. 2–3

1972 *Wetzeliella* (*Wetzeliella*) *symmetrica* Weiler var.; Benedek; p. 17, pl. 3, fig. 10*a*, *b*.

Derivation of name. This species has been named after Dr. Hans Gocht.

Diagnosis. A species of *Wetzeliella* (*Wetzeliella*) with usually subpentagonal tests.

Endoblast following closely the periblast outline but leaving a narrow and well-defined pericoel. All horns reduced to short, blunt projections or absent. The right antapical horn, when present, is markedly shorter than the left antapical horn. Abundant processes, variable in shape, usually rather flexible, open or closed distally.

Type locality. Rupel Clay (Middle Oligocene), 30 m above base, Belgium.

Holotype. T 36/2, slide ML 1194, rep. Micropalaeontology Laboratory, Department of Geology, University of Sheffield.

Dimensions. Holotype: over-all tract length 113 μ, breadth 108 μ; endoblast length 97 μ, breadth 93 μ; apical horn 0 μ; lateral horns 6 μ; antapical horn right 10 μ, left 5 μ; processes length 6–15 μ. Observed range: over-all length 118–107 μ, breadth 111–98 μ; apical horn 13–0 μ; lateral horns 10–4 μ; antapical horn right 12–5 μ, left 5–0 μ; processes length 5–18 μ. Number of specimens measured: six.

Description. Due to the variable development of the horns, the tracts may be subpentagonal, subrhombic, or subcircular, pentagonal outlines being dominant; in all cases the outline is rounded. The horns, when present, are very short, broad, and blunt. The endophragm lies close to the periphragm but there is always a well-defined, although narrow, pericoel, often continuous around the endoblast. The processes vary in shape and characters of the distal endings. Most commonly they are thin-walled, flexible, and frequently with tapering bases. They may be open or closed distally; when open, the distal margin is aculeate or entire, when closed, the distal ending is simple, acuminate, or capitate. In all the specimens observed the opercula are *in situ* and the archeopyle sutures are frequently difficult to observe.

Remarks. This species resembles *W.* (*W.*) *symmetrica* in the flexible, usually thin-walled processes, but differs from it by having all horns reduced or absent and a more rounded and commonly subpentagonal outline in contrast to the rhombic outlines with four well-developed horns characteristic of *W.* (*W.*) *symmetrica*. Some subcircular individuals of this species resemble *W.* (*A.*) *homomorpha*, from which they are distinguishable by the well-defined pericoel. *W.* (*W.*) *ovalis* also has reduced horns and rounded outlines, but its antapical horns are of about the same length and its processes are shorter, usually thicker-walled, and more rigid than in *W.* (*W.*) *gochtii*.

EXPLANATION OF PLATE 92

Fig. 1. *Wetzeliella* (*Apectodinium*) *paniculata* sp. nov. Holotype ×500.

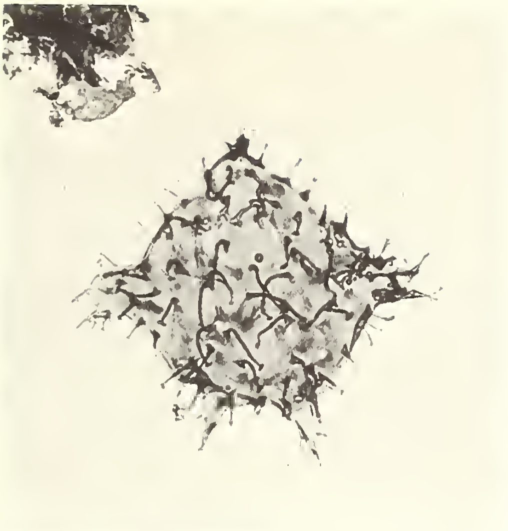
Fig. 2. *Wetzeliella* (*Wetzeliella*) *gochtii* sp. nov. Holotype ×500.

Fig. 3. *Wetzeliella* (*Wetzeliella*) *gochtii* sp. nov. Specimen from the Hamstead Beds, Isle of Wight. ×500.

Fig. 4. *Wetzeliella* (*Wetzeliella*) sp. aff. *articulata* Eisenack. Bracklesham Beds, Hengistbury Head, Hampshire. ×500.

Fig. 5. *Wetzeliella* (*Rhombodinium*) *perforata* Jan du Chêne and Chateauneuf. Middle Headon Beds, Whitecliff Bay, Isle of Wight. ×500.

Fig. 6. *Wetzeliella* (*Apectodinium*) *hyperacantha* Cookson and Eisenack, Woolwich Beds, Bean, Kent. ×500.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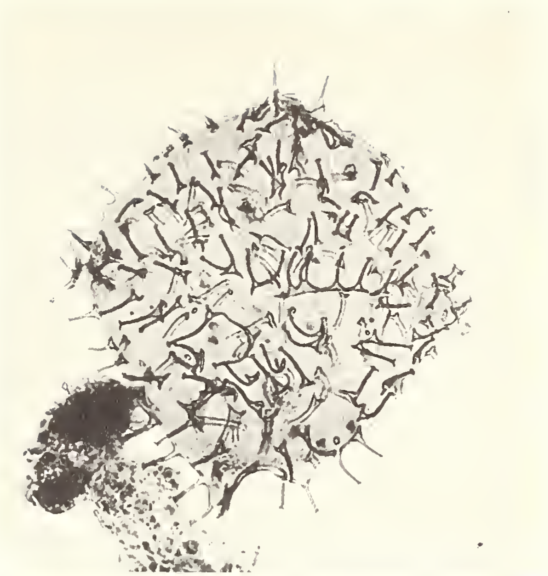
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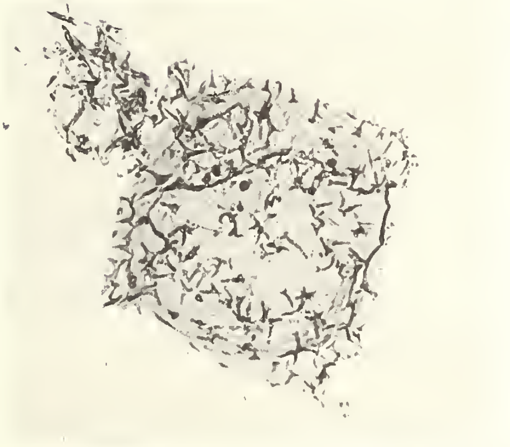
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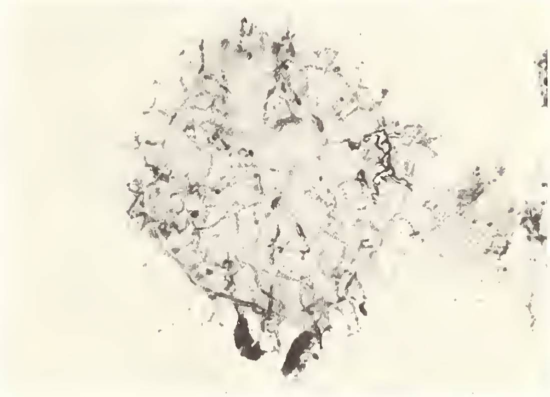
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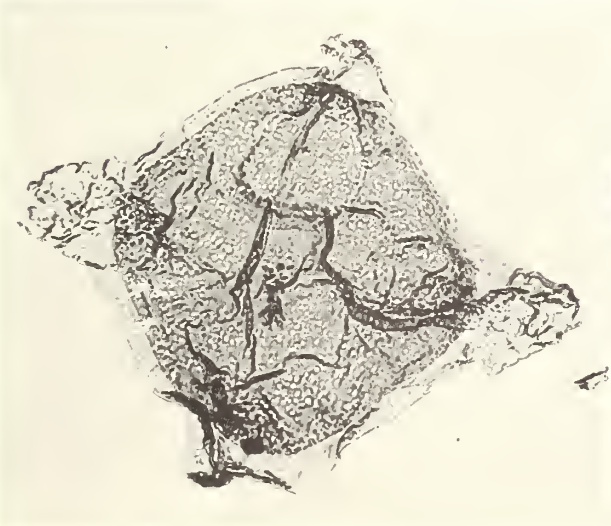
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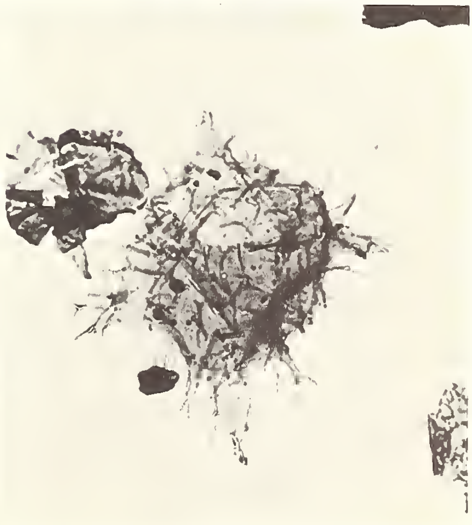
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COSTA and DOWNIE, *Wetzeliella*

Wetzeliella (*Wetzeliella*) aff. *articulata*

Plate 92, fig. 4

Remarks. These forms are smaller than *W.* (*W.*) *articulata*, with usually very thin walls and all horns reduced. The processes are also thin-walled and quite flexible, and their distal margins are very variable. These may be aculeate (the aculei sometimes uniting neighbouring processes), secate, or bear fragments of a distal reticulum or membrane. In all the specimens observed the operculum is *in situ* and the archeopyle sutures, when at all observable, are very faint. *W.* (*W.*) *articulata* is almost always present in the same assemblages where the present forms occur, as well as, sometimes, *W.* (*W.*) *coleothrypta* and *W.* (*W.*) *reticulata*; transitional forms to *W.* (*W.*) *articulata* are not uncommon. The characters of *W.* (*W.*) aff. *articulata*, particularly the fact that the archeopyle sutures are only faintly marked on the periphragm and are often incomplete, appear to suggest that these forms may be abnormally developed cysts of *W.* (*W.*) *articulata* or a related species.

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APPENDIX—LIST OF *WETZELIELLA* SPECIES

Subgenus *Wetzeliella* (*Apectodinium*) subgen. nov.

* *W.* (*A.*) *homomorpha* subsp. *homomorpha* Deflandre and Cookson, 1955
W. (*A.*) *homomorpha* subsp. *quinquelata* (Williams and Downie, 1966)
W. (*A.*) *hyperacantha* Cookson and Eisenack, 1965
W. (*A.*) *paniculata* sp. nov.
W. (*A.*) *parva* Alberti, 1961

Subgenus *Wetzeliella* (*Wetzeliella*) Eisenack, 1938, emend. Williams and Downie, 1966

* *W.* (*W.*) *articulata* Eisenack, 1938
W. (*W.*) *clathrata* Eisenack, 1938
W. (*W.*) *clathrata* subsp. *fasciata* (Rozen, 1965)
W. (*W.*) *coleothrypta* Williams and Downie, 1966
W. (*W.*) *condylos* Williams and Downie, 1966
W. (*W.*) *edwardsi* Wilson, 1967
W. (*W.*) *gochtii* sp. nov.
W. (*W.*) *lunaris* Gocht, 1969
W. (*W.*) *meckelfeldensis* Gocht, 1969
W. (*W.*) *ovalis* Eisenack, 1954
W. (*W.*) *pachyderma* Caro, 1973
W. (*W.*) *reticulata* Williams and Downie, 1966
W. (*W.*) *samlandica* Eisenack, 1954
W. (*W.*) *similis* Eisenack, 1954
W. (*W.*) *solida* (Gocht, 1955) Williams and Downie, 1966
W. (*W.*) *symmetrica* Weiler, 1956
W. (*W.*) *tenuivirgula* Williams and Downie, 1966
W. (*W.*) *tenuivirgula* subsp. *crassoramosa* (Williams and Downie, 1966)
W. (?*W.*) *unicaudalis* Caro, 1973
W. (*W.*) *varielongituda* Williams and Downie, 1966

Subgenus *Wetzeliella* (*Rhombodinium*) (Gocht, 1955) Alberti, 1961

* *W.* (*R.*) *draco* (Gocht, 1955) Alberti, 1961
W. (*R.*) *glabra* Cookson, 1956
W. (*R.*) *longimanum* Vozzhennikova, 1967
W. (*R.*) *perforata* Jan du Chêne and Chateauneuf, 1975

THE AFFINITIES OF TWO ENDEMIC SILURIAN BRACHIOPODS FROM THE DINGLE PENINSULA, IRELAND

by M. G. BASSETT, L. R. M. COCKS, *and* C. H. HOLLAND

ABSTRACT. Two endemic brachiopods are described from the Wenlock of the Dingle Peninsula, south-western Ireland: *Rhipidium hibernicum* sp. nov. and *Spirifer bigugosus* M'Coy, 1846, the latter designated as the type species of a new genus *Holcospirifer* erected here and referred to the Kozlowskiellinae.

SOME reconstructions of the North Atlantic area in Wenlock times (e.g. Mitchell and McKerrow 1975) show what is now the Dingle Peninsula (County Kerry, south-western Ireland) on the northern side of the Proto-Atlantic Ocean; other interpretations (e.g. Holland 1969*b*) place it on the southern margin. Current progress in Irish Silurian research is not yet conclusive on this point. The Dingle Peninsula yields one of the few Wenlock shelly faunas from Ireland, including rich assemblages of brachiopods, together with less common corals, molluscs, trilobites, etc. The Proto-Atlantic appears to have been closing at this time, and, in general, the brachiopod faunas were similar on both its northern and southern margins during most of the Silurian. Thus it is important in progress towards palaeogeographical understanding to document the few occurrences of endemic faunas in the region.

Silurian brachiopods were first described from Dingle by M'Coy (1846), who reported thirty-four species from the area. The fauna has not yet been fully monographed, but from stratigraphical accounts and faunal lists (e.g. Gardiner and Reynolds 1902) it has long been recognized that the assemblages are closely comparable with those from the type Wenlock and Ludlow successions of the Welsh Borderland, with the majority of species common to both areas. These relationships have been confirmed by one of us (Holland 1969*b*) in a preliminary revision of the stratigraphy. However, a number of earlier authors have quoted F. R. C. Reed's (*in* Gardiner and Reynolds 1902) identifications of *Pentamerus oblongus* (J. de C. Sowerby), *Stricklandia lens* (J. de C. Sowerby), and *S.* [= *Costistricklandia*] *lirata* (J. de C. Sowerby) as indicating a Llandovery age for part of the succession in the peninsula. These records are probably a result of misidentifications of post-Llandovery forms such as *Meristina obtusa* (J. Sowerby), ribbing of large *Atrypa* (tectonically flattened and drawn out), *Rhipidium*, and perhaps rhynchonellids. The oldest beds in the Dingle Peninsula are now known to be no older than Wenlock (Holland 1969*a*, *b*).

Within the Wenlock succession there are two distinctive brachiopod species, each very common and dominating its local assemblage at certain localities, which are not known from elsewhere and appear to be endemic to the Dingle area. They have been fairly widely quoted as *Spirifer bijugosa* M'Coy, 1846 [note the misspelling], from the Ferriters Cove and Clogher Head formations, and *Rhipidium* sp., from the

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stratigraphically higher Drom Point Formation; but their affinities and taxonomic relationships with other species have remained obscure. Both species are described in full here so as to clarify these relationships.

The Silurian succession in the western, Clogher Head, inlier of the Dingle Peninsula includes a substantial amount of volcanic rocks, especially in the Clogher Head Formation but also in the Ferriters Cove Formation below and the Mill Cove Formation above (both also Wenlock in age). Volcanic rocks are also prominent in the Wenlock rocks of Inishvickillane, the south-westernmost of the Blasket Islands, off the end of the peninsula and some 15 km south-west of Clogher Head. Neither of the two brachiopod species described here is present in the Wenlock rocks of the Annascaul inlier of the south-eastern part of the Dingle Peninsula some 20–40 km east of Clogher Head (see Holland 1969*b*, fig. 5 or Parkin 1974, fig. 1). Parkin has found there only relatively thin volcanic mud flows and tuff beds. Neuman (1972) postulated volcanic islands as centres of evolution during the lower Ordovician and Cocks and McKerrow (1973) have suggested a similar relationship in the Wenlock of Bohemia. Thus the Dingle brachiopods described here may have been products of the same process, bearing in mind, however, that associated with these endemic species are other forms of wider distribution.

Most of the material described here is deposited in the Geological Museum of Trinity College, Dublin (TCD), though a few specimens are from the National Museum of Ireland (NMI) and the British Museum (Natural History) (BB).

Superfamily PENTAMERACEA M'Coy, 1844
Family PENTAMERIDAE M'Coy, 1844
Subfamily PENTAMERINAE M'Coy, 1844
Genus RHIPIDIUM Schuchert and Cooper, 1931

Type species. Pentamerus Knappi Hall and Whitfield, 1872, p. 3, from the Silurian of Louisville, Kentucky, U.S.A.

Rhipidium hibernicum sp. nov.

Plate 93, figs. 1–6; Plate 94, figs. 1–5

1863 *Pentamerus Knightii* J. Sowerby; Salter, p. 13 [name only: *non* J. Sowerby, 1812].
1867 *Pentamerus Knightii* J. Sowerby; Davidson, p. 142 *pars*, pl. 19, fig. 3, *non* pl. 16, figs. 1–3, *non* pl. 17, figs. 1–10 [*non* J. Sowerby, 1812].
1965 *Rhipidium* aff. *pingue* Amsden; Lamont, p. 20 [*non* Amsden, 1949].
v1969*a* *Rhipidium* sp. Holland, p. 210 [name only].
v1969*b* *Rhipidium* aff. *pinque* [*sic*] Amsden; Holland, p. 305 [name only: *non* Amsden, 1949].
v1974 *Rhipidium* sp. Parkin, p. 284 [name only].

Holotype. TCD 13646a, b, internal mould of pedicle valve and counterpart external mould; Plate 93, fig. 1*a*–*d*; from the Drom Point Formation (Wenlock), northernmost cliffs of Great Blasket Island.

Paratypes. TCD 13647–13654, from the same horizon and locality as the holotype; BB 36919 and 36921, Drom Point Formation, Dunquin river 470 m north-east of the bridge where the main road crosses the river.

Diagnosis. Gently biconvex *Rhipidium* with a weakly incurved ventral beak, large triangular inner plates, and very long, slender outer plates which fuse posteriorly with the brachial processes. Spondylium entirely supported on high septum which passes anteriorly into a long slender myophragm. Radial ornament fairly coarse.

Description

Exterior. Ventribiconvex, with the pedicle valve weakly to moderately curved and the brachial valve only gently curved posteriorly, and almost flat anteriorly in some specimens. Both valves are evenly curved (non-lobate) transversely. Outline broadly subtriangular, hinge line very short and curved, merging smoothly with long, straight to gently curved posterolateral margins; maximum width close to mid-length, anterolateral and anterior margins evenly curved. Anterior commissure rectimarginate and crenulate. Interareas very short or lacking, ventral beak suberect or weakly curved up to, but not crossing, the hinge line. Delthyrium apparently open, delthyrial angle 60–70°. Radial ornament coarsely costellate; costae rarely bifurcate before the 10 mm growth stage, and throughout growth branching is not common, but does occur, mainly close to the mid-line. Ribs strong, even and rounded in section; there are sixteen to eighteen ribs at the 20 mm growth stage of the pedicle valve, with rib-width increasing anteriorly to over 2 mm, separated by rounded interspaces of about the same width. Faint, slightly lamellose concentric growth fila are visible in some shells.

Pedicle valve interior. Spondylium duplex well developed, deep, broad, with lateral plates widely flared outwards to join the posterolateral walls of the valves, enclosing deep lateral cavities; the spondylium may occupy up to a quarter valve length, and is supported throughout its length by a high, slender septum, whose height decreases abruptly below the anterior end of the spondylium to form a low myophragm extending anteriorly for over half the valve length, sometimes as much as 80% of the length. Musculature not observed.

Brachial valve interior. Inner plates broad, triangular, flared widely laterally to join the valve walls. Brachial processes slender, restricted to the posterior third of the valve, supported throughout their length by, and fused with, slender outer plates which are subparallel or slightly divergent anteriorly, and extend beyond the processes for up to 80–90% of the valve length. Both brachial processes and outer plates are inclined slightly ventrolaterally on to the floor of the valve. Musculature not observed.

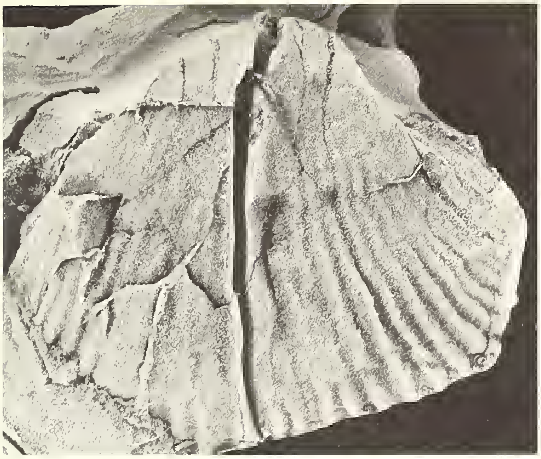
Dimensions. All the available specimens are too fragmentary to give accurate dimensions, but mature shells reached a length of more than 50 mm and a width of about 45 mm.

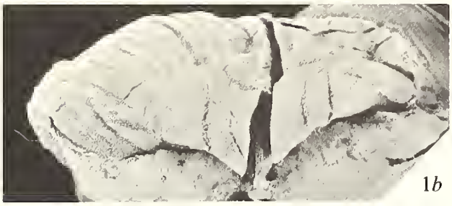
Discussion. *Rhipidium hibernicum* is the only known species of *Rhipidium* in the British Isles. A record of the genus by Ziegler *et al.* (1968) in the early Wenlock Nash Scar Limestone of Powys, Wales, can probably be discounted (for discussion see Bassett 1976). The Dingle form was first correctly referred to the genus by Dr. A. Lamont, who informally published the attribution in a Ludlow Research Group Bulletin in 1955. *R. hibernicum* differs from the type species *R. knappi* in being less strongly biconvex and in having fewer bifurcating ribs, while *knappi* is also distinguished in being distinctly trilobate anteriorly. *R. knappi* has an average of thirty-eight ribs at 40 mm length, as compared with twenty-six in *R. hibernicum. R. pingue* Amsden, 1949, from the Brownsport Formation (Ludlow) of Tennessee, U.S.A., with which *hibernicum* has been compared in the past (see synonymy), differs in having coarser, more angular ribs, much shorter outer plates, and less widely flared inner plates, and a shorter ventral septum. The approximately contemporaneous *R. tenuistriatum* (Lindström, 1880) from the Slite Beds (Wenlock) of Gotland, Sweden, differs from *hibernicum* in its stronger convexity, more strongly incurved ventral beak, less coarse ribbing, and shorter ventral septum and outer branchial plates.

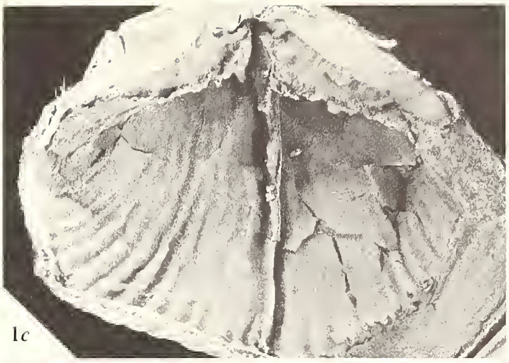
Occurrence. Unlike *Holcospirifer bigugosus*, which is found at many localities and various horizons in the Wenlock rocks of the Dingle Peninsula, *R. hibernicum* is recorded from only four places and seems to be restricted stratigraphically to a particular upper Wenlock horizon. Substantial collections have been obtained from the cliff section at the northern extremity of the Great Blasket Island, where a small area of fossiliferous rocks of the uppermost Drom Point Formation is in faulted contact with the fluviatile sediments of the Dingle Group which form the bulk of the island. Preservation is in a strikingly ochrous decalcified siltstone in some beds of which moulds of *Rhipidium* are the dominant fossil; although mostly fragmentary, the specimens here are undistorted and unflattened. These beds succeed and are associated with *Chondrites* bearing beds, which are also present on the coastal sections of the adjacent mainland of the peninsula where the *Rhipidium* bank is faulted out. The same *Rhipidium*-rich beds, though in a less decalcified condition, are found inland in the Dunquin river 470 m north-east of the bridge where the main road crosses the river. The distinctive lithology again suggests a particular facies control. Here the *Rhipidium* horizon at the top of the Drom Point Formation is succeeded by the Croaghmarhin Formation which yields both uppermost Wenlock and Ludlow faunas. The *Rhipidium* which Davidson (1867, pl. 19, fig. 3) figured as *Pentamerus knightii* is given as from Ballyaglish, east of Ferriters Cove, Dingle. The actual exposure has not been located but the position of Ballyaglish within the Clogher Head inlier is structurally consistent with the horizon exposed on the Great Blasket and in the Dunquin river. Finally Parkin (1974) has recorded two specimens of *Rhipidium*

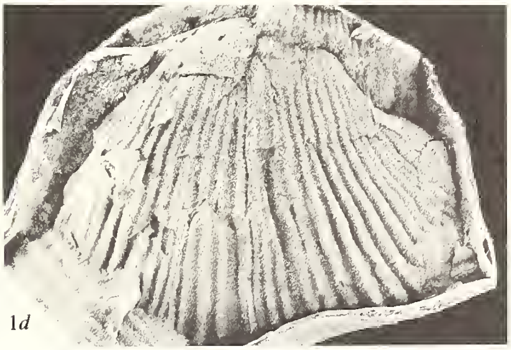
EXPLANATION OF PLATE 93

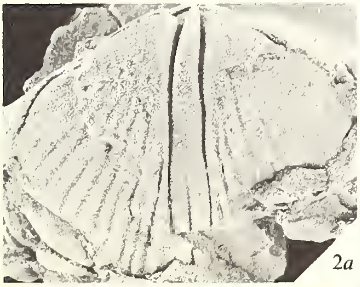
Figs. 1–6. *Rhipidium hibernicum* sp. nov. 1*a–d*, ventral view of internal mould of pedicle valve, posterior view, latex cast, and latex cast of counterpart external mould, holotype, TCD 13646a, b, Drom Point Formation (Wenlock), northernmost cliffs of Great Blasket Island. 2*a–d*, dorsal view of internal mould of brachial valve, latex cast, posterior view of mould, and enlargement of cast to show the brachial apparatus with long, slender, outer plates, broad, triangular inner plates, and short brachial processes fused to outer plates, paratype, TCD 13647, same horizon and locality as holotype. 3, internal mould of brachial valve showing long, subparallel outer plates of brachial apparatus, paratype, TCD 13648, same horizon and locality as holotype. 4, longitudinal section through mould of umbonal region of pedicle valve showing the spondylium and supporting septum, and the gentle curvature of the beak, paratype, BB 36919, Drom Point Formation, Dunquin river 470 m north-east of the bridge where the main road crosses the river. 5, internal mould of pedicle valve, paratype, TCD 13649, same horizon and locality as holotype. 6, latex cast of external mould of brachial valve showing trace of outer plates, paratype, TCD 13650, same horizon and locality as holotype. Fig. 2*d* × 4, all other figs. × 1·5.

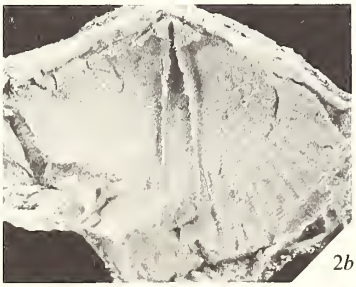

1*a*

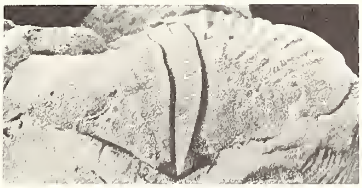

1*b*

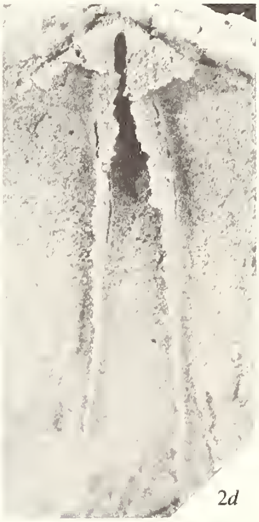

1*c*

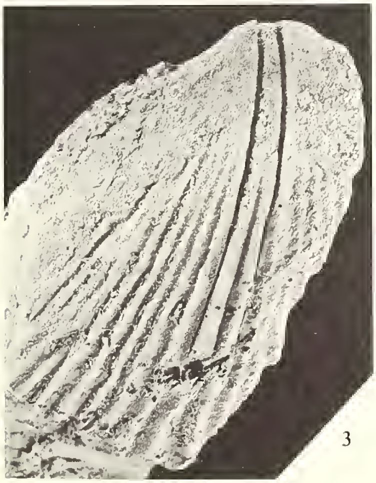

1*d*


2*a*


2*b*


2*c*


2*d*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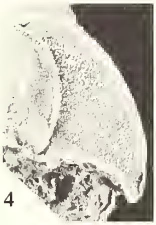
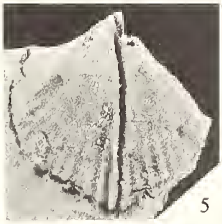
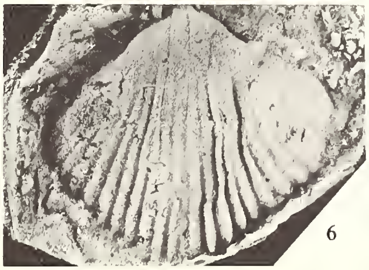

4


5


6

BASSETT, COCKS and HOLLAND, *Rhipidium hibernicum* from the lower part of the upper Wenlock Landing Place Formation on the island of Inishvickillane, where they are associated with *Chondrites* smaller than those seen in the Clogher Head inlier.

Superfamily SPIRIFERACEA King, 1846
Family DELTHYRIDAE Waagen, 1883
Subfamily KOZLOWSKIELLINAE Boucot, 1957
Genus HOLCOSPIRIFER gen. nov.

Derivation of name. From the Greek 'holcos' meaning groove, referring to the nature of the fold.

Type species. Spirifer bigugosus M'Coy, 1846.

Diagnosis. Kowslowskielline with a plicate fold and lacking a ventral median septum.

Species assigned. Spirifer bigugosus M'Coy, 1846—described here.

Spirifer sulcata var. *elongata* Munthe, 1910, from the Eke Beds (Ludlow) of Gotland, Sweden.

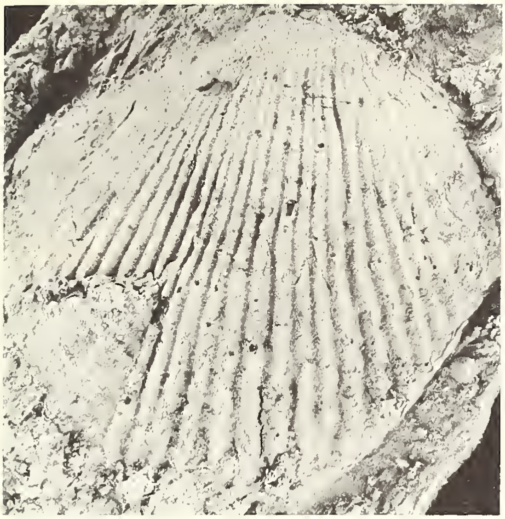
Spirifer insignis Hedström, 1923, from the Klinteberg and Hemse Beds (late Wenlock and Ludlow) of Gotland, Sweden.

Discussion. Only two other kozlowskielline genera are known. *Holcospirifer* is most closely related to *Boucotinskia* Brunton and Cocks, 1967, but differs in having a plicate fold and sulcus, in the same way as the eospiriferid *Nikiforovaena* differs from *Striispirifer*. *Boucotinskia* has a non-plicate fold and sulcus (Bassett and Cocks 1974, pl. 11, fig. 2). Both *Holcospirifer* and *Boucotinskia* differ from *Kozlowskiellina* Boucot, 1958 in lacking a ventral median septum. Bassett and Cocks (1974, p. 39) regarded the Gotland *insignis* as a subspecies of *elongata*, and included them questionably within *Boucotinskia*. Both have a plicate fold and sulcus, and are thus assigned here to *Holcospirifer*.

EXPLANATION OF PLATE 94

Figs. 1–5. *Rhipidium hibernicum* sp. nov. 1, latex cast of external mould of pedicle valve, paratype, TCD 13651, same horizon and locality as holotype. 2*a*, *b*, ventral and lateral views of internal mould of pedicle valve showing the gentle curvature of the beak, paratype, TCD 13652, same horizon and locality as holotype. 3, internal mould of posterior portion of brachial valve, paratype, BB 36921, horizon and locality as for BB 36919. 4, latex cast of internal mould of pedicle valve showing long septum supporting the spondylium, paratype, TCD 13653, same horizon and locality as holotype. 5*a*–*c*, internal mould of pedicle valve, latex cast of median area, and posterior view of median area of mould, paratype, TCD 13654, same horizon and locality as holotype. All ×1·5.

Figs. 6–8. *Holcospirifer bigugosus* (M'Coy, 1846). 6*a*, *b*, dorsal and posterior views of internal mould of brachial valve, lectotype, NMI G3/1. 1975, Sir Richard Griffith Collection, from Ferriters Cove. Specimen kindly loaned by the Director, National Museum of Ireland. 7*a*, *b*, external mould of pedicle valve and latex cast, TCD 13655, Ferriters Cove Formation, Coonakeel, north side of Ferriters Cove, 290 m east of Ferriters Castle. 8*a*, *b*, internal mould of brachial valve and latex cast, TCD 13656, Ferriters Cove Formation, north side of Ferriters Cove, 290 m east-north-east of previous locality. All ×1·5.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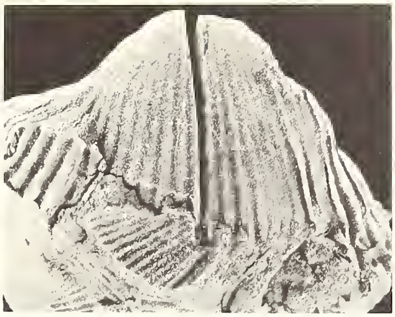
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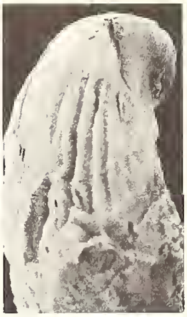
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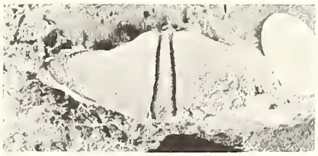
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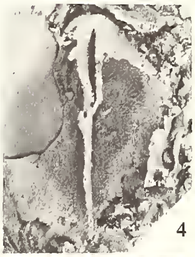
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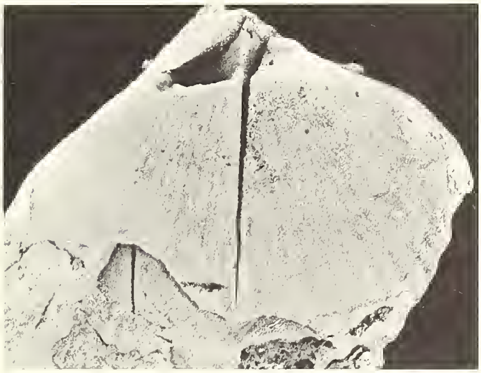
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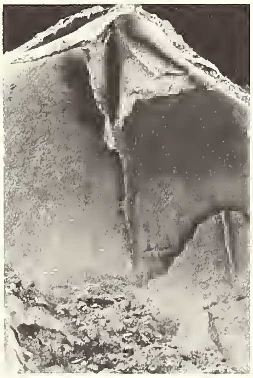
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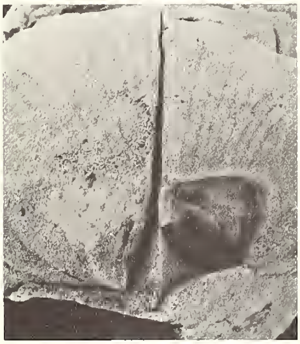
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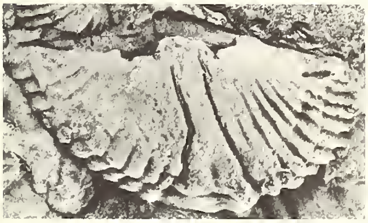
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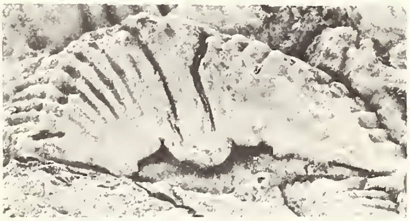
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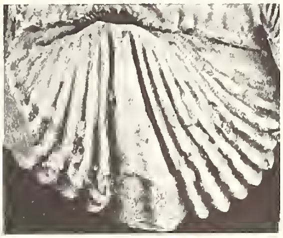
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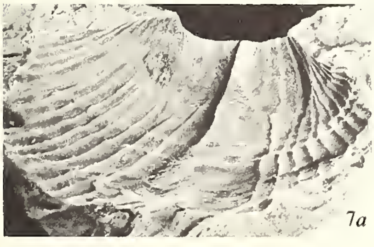
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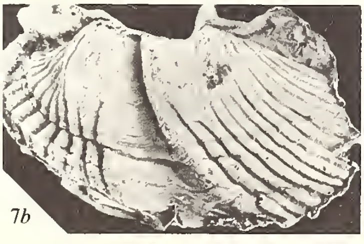
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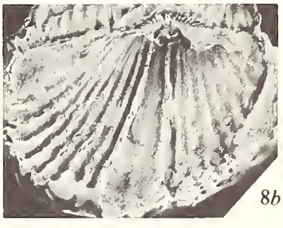

8*b*

BASSETT, COCKS and HOLLAND, *Rhipidium hibernicum* and *Holcospirifer bigugosus*

Holcospirifer bigugosus (M'Coy, 1846)

Plate 94, figs. 6–8; Plate 95, figs. 1–6

v1846 *Spirifer bigugosa* M'Coy, p. 36, pl. 3, fig. 23 [*Spirifer bigugosus* [*sic*] in plate legend].
v1862 *Spirifer bigugosa* M'Coy, p. 36, pl. 3, fig. 23 [second edition, unchanged].
1863 *Spirifera bijugosa* (M'Coy); Salter, p. 13 [name only].
1867 *Spirifera bijugosa* (M'Coy); Davidson, p. 89, pl. 10, figs. 1–3.
1902 *Spirifer bijugosus* M'Coy; Gardiner and Reynolds, pp. 234 et seq. [name only].
v1969*b* *Macropleura bijugosa* (M'Coy); Holland, pp. 302, 304 [name only].

Type locality. M'Coy (1846, p. 36) recorded this fossil as 'very abundant in the shales of Doonquin, Dingle, County Kerry; very common in the slates of Ferriter's Cove, Dingle, Co. Kerry'. The Ferriters Cove Formation and Clogher Head Formation (both Wenlock) are well exposed in Ferriters Cove and the 'Doonquin' reference is to the latter (Holland 1969*b*). The species is widely distributed in both formations.

Type specimens. M'Coy described the collection of Sir Richard Griffith, now in the National Museum of Ireland. Only one block containing specimens of *bigugosus* (and regarded as type material) is now available from this collection (NMI G3. 1975). Although none of the specimens on the block can be identified directly with M'Coy's illustration (which was probably a reconstruction), nevertheless they are syntypes, and we here select as lectotype NMI G3/1. 1975 (Plate 94, fig. 6*a*, *b*). The locality is simply given as 'Ferriter's Cove'.

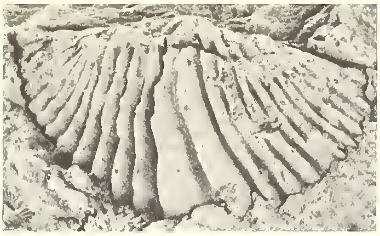
Other material. TCD 13655 Ferriters Cove Formation, Coonakeel (literally 'bay of the narrow', though the locality is on a small headland), north side of Ferriters Cove, 290 m east of Ferriters Castle; TCD 13656 Ferriters Cove Formation, north side of Ferriters Cove, 290 m east-north-east of previous locality; TCD 13657–13658 Clogher Head Formation, clifftop exposure west of Dunquin and 220 m north of Redcliff Cove; TCD 13659–13661 Clogher Head Formation, Ferriters Cove (detailed localities unknown).

Description

Exterior. Ventribiconvex; valves elliptical in outline, half to two-thirds as long as wide, maximum width just anterior to the hinge line. Ventral beak suberect, ventral interarea long, curved, apsacline, with large open delthyrium flanked by thin detached delthyrial plates. Delthyrial angle about 40°. Dorsal interarea very short. Radial ornament plicate and fimbriate; ribs subangular in cross-section, with five to fifteen (mode 10) non-branching, equally spaced lateral plicae on either side of the fold and sulcus, which are prominent, widening anteriorly, with a central groove in the fold and a faint complementary plication in the sulcus. Concentric ornament fine,

EXPLANATION OF PLATE 95

Figs. 1–6. *Holcospirifer bigugosus* (M'Coy, 1846). 1, internal mould of brachial valve, syntype on same slab as lectotype, NMI G3/3.1975, Sir Richard Griffith Collection, from Ferriters Cove. 2*a*–*d*, dorsal, ventral, anterior, and posterior views of steinkern, TCD 13657, note the distinctive groove on the dorsal fold, Clogher Head Formation, clifftop exposure west of Dunquin and 220 m north of Redcliff Cove. 3*a*–*c*, external mould of pedicle valve, latex cast, and enlargement of part of cast to show kozlowskiellinid ornament, TCD 13659, Clogher Head Formation, Ferriters Cove. 4*a*–*d*, internal mould of brachial valve and latex cast, counterpart external mould and latex cast, TCD 13660a, b, Clogher Head Formation, Ferriters Cove. 5*a*–*c*, internal mould of pedicle valve and latex cast, and oblique view of cast showing the high, distinctive dental plates, TCD 13658, horizon and locality as for TCD 13657. 6*a*–*d*, ventral and posterior views of internal mould of pedicle valve, latex cast, and oblique view of cast showing shape of dental plates, TCD 13661, Clogher Head Formation, Ferriters Cove. Fig. 3*c* ×4, all other figs. ×1·5.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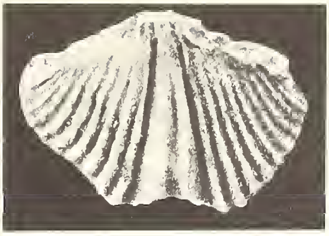
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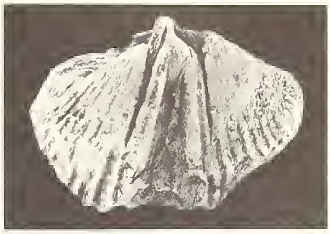
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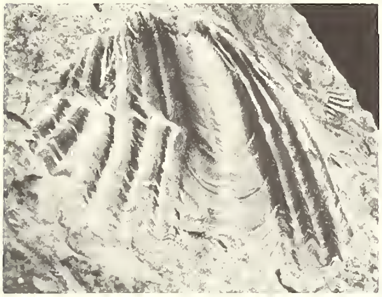
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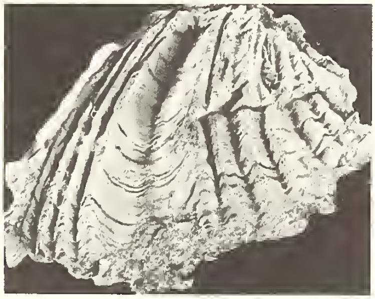
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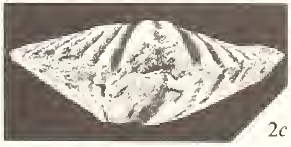
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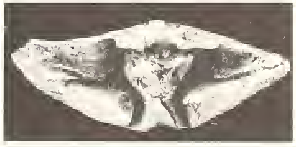
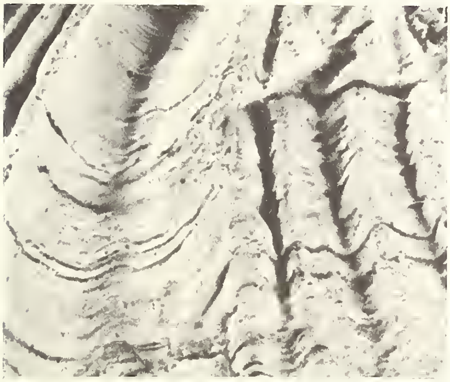

2*d*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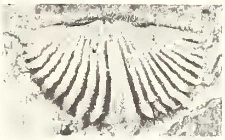
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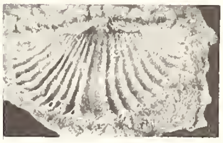
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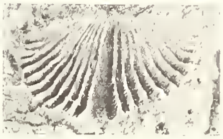
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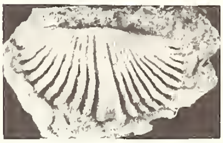
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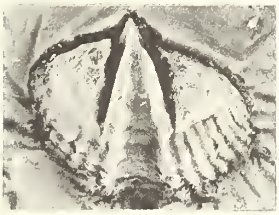
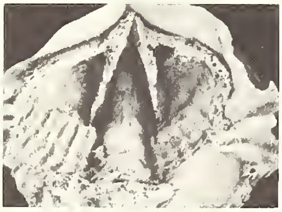

5*a*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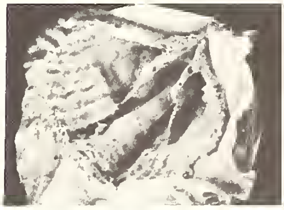
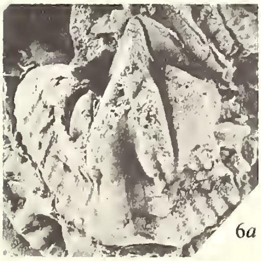
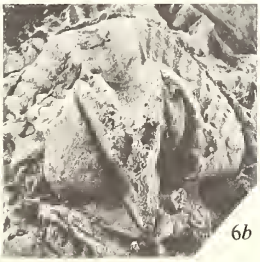

5*c*


6*a*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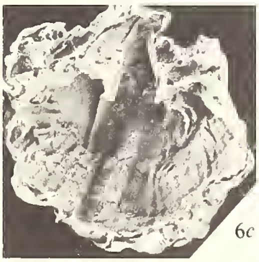
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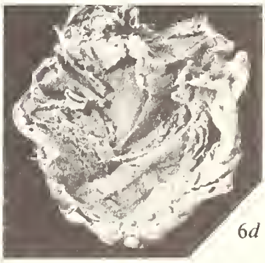
6*d*

BASSETT, COCKS and HOLLAND, *Holcospirifer bigugosus* lamellose, sometimes accentuated at coarse growth stages. Although most specimens are poorly preserved, very fine radially aligned spines cross the growth lamellae, giving the appearance of a fine eospiriferid-like radial ornament in places.

Pedicle valve interior. Teeth small, cyrtomatodont, rounded and slightly curved, supported by prominent dental plates which diverge at an angle of approximately 40°, drop abruptly below the teeth, and then decrease in height to join the floor of the valve at about mid-valve length. The teeth and plates are straight and bound deep lateral cavities which are undercut below the interarea, and in a few gerontic specimens include secondary calcite posterolaterally. There is no median septum. Muscle scars obscure, but suboval and confined to the posterior area between the dental plates.

Brachial valve interior. Notothyrial cavity shallow and longitudinally striated in some specimens, with a very small central process. Sockets small, shallow, bounded laterally and dorsally by wide hinge plates and medially by short crural plates. There is no median septum. The notothyrial platform extends for a short distance anteriorly as a broad, low ridge which tapers anteriorly between the impression of the fold. Form of spiralia and musculature unknown.

Dimensions. The material in this case is distorted, but large specimens of *H. bigugosus* must have exceeded 25 mm in length and 40 mm in width.

Discussion. The slightly younger *H. elongatus* (and its subspecies *insignis*) differs from *H. bigugosus* in its stronger concentric ornament. It is also more alate, with more sharply pointed extremities (Bassett and Cocks 1974, pl. 11, figs. 3–7), the fold is more strongly grooved, and the sulcus contains a pair of plications in some specimens.

This paper is a contribution to Project Ecostratigraphy.

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JURASSIC FLORAS OF THE KARATAU RANGE, SOUTHERN KAZAKHSTAN

by M. P. DOLUDENKO *and* E. R. ORLOVSKAYA

ABSTRACT. A series of six rich floras, containing about 180 plant species, is known from the upper part of the Lower Jurassic (Upper Liassic), the Middle Jurassic, and the Upper Jurassic of Kazakhstan. An analysis of the composition of these floras reveals gradual changes which may be correlated with changes in the climate and palaeogeography of the region. The data on Upper Jurassic megafossil floras is compared with that on their spores and pollen.

THE study of Jurassic floras of the Karatau Range (southern Kazakhstan), a north-western spur of the Tien Shan Mountains, began about 50 years ago in connection with intensive research on Jurassic deposits and prospecting for coal in this region. Palaeobotanical materials from the Karatau were examined by Romanovsky (1890), Seward (1907), Brick (1925*a–c*), Turutanova-Ketova (1929, 1930, 1936*a*, *b*, 1950, 1963), Prinada (in Buvalkin 1958), Vakhrameev and Yaroshenko (1958), Romanova (1961), and Murakhovskaya (1968). In the 1960s Sakulina, studying spore-pollen assemblages from Jurassic deposits of the Karatau Range, noticed that the correlation and dating of Jurassic strata, particularly of those from the Lower and Middle Jurassic, were not precise enough. She invited Orlovskaya to take part in analysing the floristic materials. Shortly after, Doludenko, who had formerly studied the Callovian[1] flora of Georgia (Doludenko and Svanidze 1968, 1969) turned to studying the Upper Jurassic flora of the Karatau. (The collections containing the flora described by Orlovskaya from the upper Lower Jurassic–Middle Jurassic are kept at the Institute of Zoology of the Academy of Sciences of Kazakhstan S.S.R. in Alma-Ata; those of the Upper Jurassic flora described by Doludenko are kept at the Geological Institute of the U.S.S.R. Academy of Sciences in Moscow.) A monographic description of the Jurassic floras of the Karatau will be published in the Transactions of the Geological Institute of the Academy of Sciences of the U.S.S.R.

Study of the Karatau Jurassic floras is of a great practical importance, as it can help to work out a general stratigraphic scheme for this region, and it also throws light on Jurassic floras in general.

The work of Turutanova-Ketova on the Upper Jurassic flora of the Karatau is particularly noteworthy. We know very few Upper Jurassic floras within the Indo-European palaeofloristic area, because in the Late Jurassic the climate became much more arid throughout much of Europe, Kazakhstan, and Middle and Central Asia. Such floras as have been described are from Scotland, France, India, Japan, and the U.S.S.R. (Georgia and the Gissarian Range). The Jurassic flora of the Karatau grew on the bank of a lake (Gekker 1948) and was buried in lake sediments, unlike those of Scotland, France, and Georgia, which were sea-coast floras.

The Karatau Range stretches over 400 km from south-east to north-west. It is subdivided into the Bolshoy and Maly Karatau, the latter being subparallel to, and

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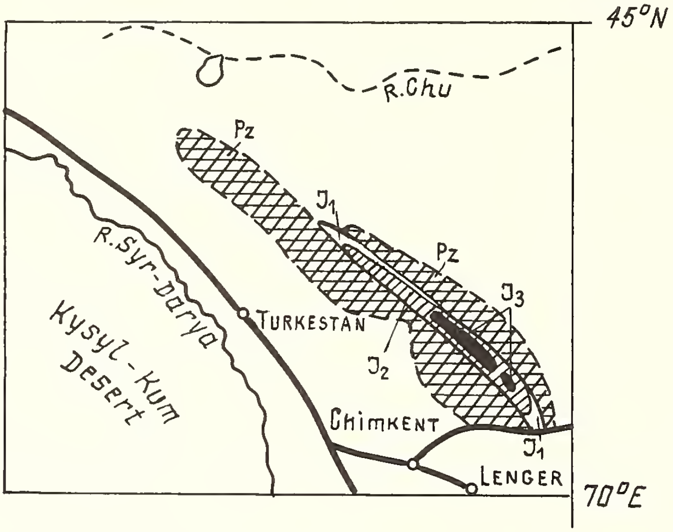
[1] The Callovian is placed, by geologists of the U.S.S.R., in the Upper Jurassic.

[Palaeontology, Vol. 19, Part 4, 1976, pp. 627–640.]

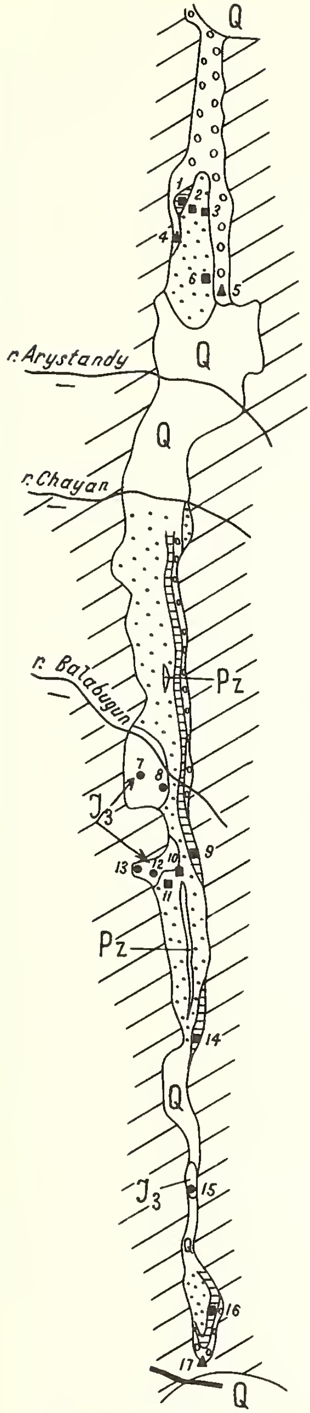
to the east of, the Bolshoy Karatau. The Karatau Range is composed of rocks of almost all geological ages, beginning with the Lower Proterozoic. Jurassic deposits form a narrow belt between the Maly Karatau and the southern and central parts of the Bolshoy Karatau (text-fig. 1). This belt, 2–8 km wide, stretches over 200 km from the Chokpak pass in the south-east to the valley of the Bala Turlan river in the north-west. The locations of the Jurassic floras of the Karatau Range are given in text-fig. 2.



TEXT-FIG. 1. Sketch of southern Kazakhstan to show location of Jurassic deposits (J_1, J_2, J_3) between Palaeozoic rocks (Pz). Thick black lines indicate railways.

Jurassic deposits in the Karatau Range were discovered in the second half of the nineteenth century. The first map of Lower and Middle Jurassic outcrops was compiled in 1904 by Veber and Bronnikov. In 1921 the engineer Aniskovich found, near the village of Galkino (now Uspenskoie), outcrops of thin foliated shales with rich remains of the Upper Jurassic fauna and flora. From then on, some interesting localities (Chugurchak, Karabastau and Aulie) were found near the village of Mikhailovka; these contain well-preserved Upper Jurassic plants, insects, fish, and flying reptiles.

The subdivision of these Jurassic deposits has been studied by various geologists and palaeontologists. It is not an easy task, as the Jurassic outcrops are separated and are all continental deposits, containing only plants, fish, and insects. The most complete stratigraphic summary of the Karatau Range was published by Gekker (1948) and Buvalkin (1960; Geology of the U.S.S.R., 1971). In 1971 Sakulina published a paper on the stratigraphy of the upper part of the Karatau Jurassic section. Study of the Jurassic of the Karatau Range continues; new boreholes have been drilled and samples have been collected for a spore-pollen analysis. Sakulina and geologists of the South Kazakhstan Geological Survey are working on the stratigraphic subdivision of the Karatau Jurassic. Sakulina prepared a preliminary new



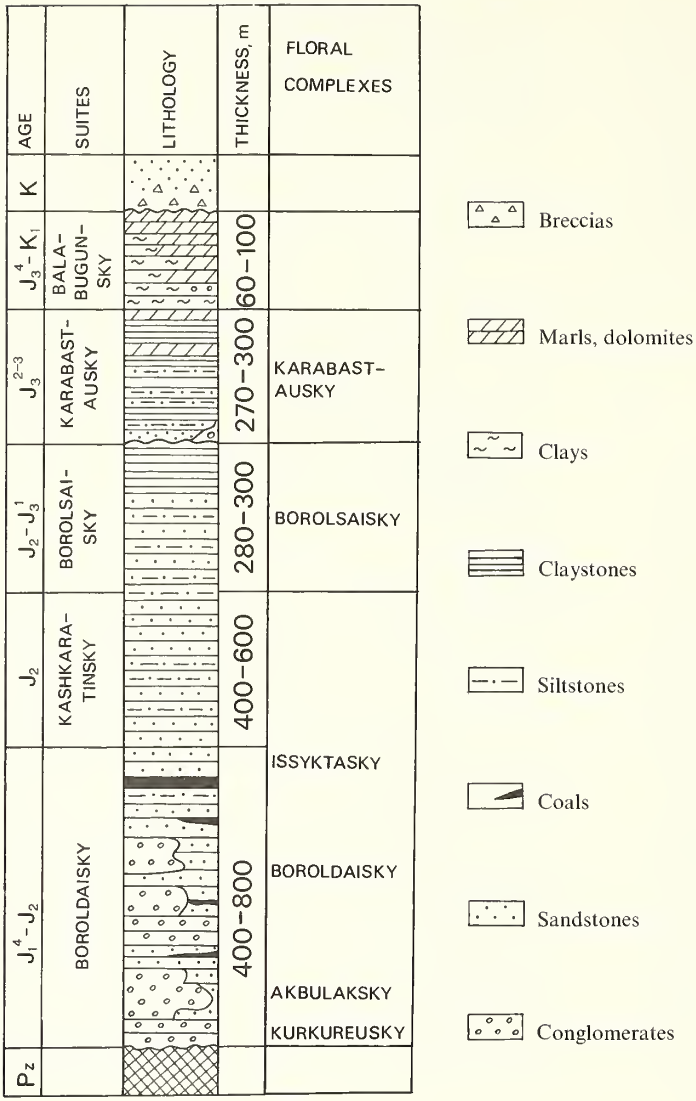
TEXT-FIG. 2. Map of Jurassic deposits indicated in text-fig. 1. Numbered localities containing Early Jurassic floras are indicated by triangles, those containing Middle Jurassic floras are indicated by squares, those containing Late Jurassic floras are indicated by circles. J_3, strata of dolomite, clay limestone, siltstone, sandstone, and combustible shales of the Upper Jurassic Borolsaisky and Karabastausky suites. Pz, Palaeozoic deposits. Q, Quaternary deposits. Dotted areas indicate strata of sandstone, siltstone, and claystone of the Middle Jurassic Boroldaisky and Kashkaratinsky suites. Horizontally lined areas indicate Middle Jurassic coal-bearing measures of the Boroldaisky suite. Open circles indicate Late Lower Jurassic conglomerate strata of the Boroldaisky suite. 1–17, localities containing Jurassic floras, as follows: 1, Taskomyrsaiskoie coal deposit and mining area; 2, Taskomyrsai ravine; 3, Taskomyrsai, exposure 5; 4, Akbulak gully; 5, Kurkureu gully; 6, Issyktas gully; 7, Karabastau; 8, Chugurchak area; 9, Ayak-Sunginskoie coal deposit; 10, Ayak-Sunga river, exposure 24; 11, Kashkarata river; 12, Chokhai area; 13, Aulie area; 14, Boroldaiskoe coal deposit; 15, village of Uspenskoie (Galkino); 16, Chokpak hard coal deposit; 17, Chokpak river (Melnichny area of the Chokpak hard coalfield).

stratigraphic scheme of the Karatau Jurassic, and kindly forwarded it to us (text-fig. 3). This shows the Karatau Jurassic beds resting uncomformably on various Palaeozoic rocks. The lowest member, here called the Boroldaisky suite, extends from the upper part of the Lower Jurassic to the Middle Jurassic. The Kashkaratinsky suite rests conformably on this and passes (also conformably) into the rocks of the overlying Borolsaisky suite. Unconformity has been recorded only between the rocks of the Borolsaisky and overlying Karabastausky suites. The latter three suites correspond to the Chockpaksky, Taskomyrsaisky, and Boroldaisky suites distinguished by Buvalkin (1960).

In these Jurassic suites it is possible to distinguish three floras, each containing two assemblages (text-fig. 3 and Appendix).

Upper Jurassic taphoflora
  Karabastausky assemblage
  Borolsaisky assemblage
Middle Jurassic taphoflora
  Issyktasky assemblage
  Boroldaisky assemblage
Lower Jurassic (late Liassic) taphoflora
  Akbulaksky assemblage
  Kurkureusky assemblage

The detailed composition of each of these six assemblages is given in the Appendix. The main features of these will now be considered in turn.



TEXT-FIG. 3. Stratigraphic scheme of Jurassic deposits of the Karatau Range, compiled by Sakulina. J_1, Lower Jurassic; J_2, Middle Jurassic; J_3, Upper Jurassic; Pz, Palaeozoic.

The Kurkureusky assemblage. This was established by Orlovskaya as occurring in interbeds of sandstone and siltstone within conglomerate strata in the Kurkureu and Betpaksu ravines and by the Chakpak river, in the Melnichny area (text-fig. 2, localities 5 and 17). Notable elements include older types of equisetalean that have persisted since considerably earlier in the Mesozoic (e.g. *Annulariopsis inopinata*), and abundant specimens of *Neocalamites*. Ferns are strongly represented, particularly species of *Cladophlebis* with large pinnules. Ginkgoalean leaves are common, and cycadophyte leaves are abundant. The presence of the conifer *Storgaardia spectabilis*, known from the Lower Liassie of Greenland, is also noteworthy.

The Akbulaksky assemblage. This was defined by Prinada (in Buvalkin 1958) as occurring in compact grey sandstones in the Akbulak gulley (text-fig. 2, locality 4). Equisetaleans, ferns, and cycadophytes are abundant, but ginkgoaleans, czekanowskialeans, and conifers are now present in a more minor role. *Neocalamites* is still present (though as a different species), but *Annulariopsis* has disappeared. The conifer *Ferganiella* is present, but we nevertheless consider the assemblage to be of late Lower Jurassic rather than Middle Jurassic age. This is because, as a whole, it resembles the Upper Liassic floras of Issyk-Kul Lake (Genkina 1966) and South Fergana (Vakhrameev 1964, 1970). Apart from *Ferganiella*, there is little in the Akbulaksky assemblage to suggest a Middle Jurassic age.

The Boroldaisky assemblage. This assemblage, rich in species, has been recognized in coal deposits of the Boroldaisky, Taskomyrsaisky, Chokpaksky, and Ayak-Sunginsky coalfields (text-fig. 2, localities 1, 2, 9, 14, 16). Romanova (1961) has described some of the species from the Boroldaisky deposits, and some of the species also occur in the Chokpaksky region (Turatanova-Ketova 1936*a*). *Equisetum* is now the dominant arthrophyte, and *Neocalamites* is now found only occasionally. There are many species of the fern *Cladophlebis*, but small-pinnuled forms now predominate. Only one specimen of *Clathropteris* has been found, but *Raphaelia* appears for the first time. Cycadophytes, particularly *Nilssoniopteris*, are common, and several gymnosperm genera are represented by species not found earlier. *Ferganiella* is the commonest conifer, but *Pityophyllum* is also frequent. The assemblage appears to be of early Middle Jurassic age.

The Issyktasky assemblage. This has been recognized in sandstones exposed in the Issyktas gulley of the Taskomyrsaisky coalfield in exposure 5 (text-fig. 2, localities 3 and 6). It also replaces the Boroldaisky assemblage higher in those sections. The Issyktasky assemblage is rather poor in species, but contains abundant specimens of *Phoenicopsis*, *Pityophyllum*, and *Pagiophyllum setosum*, and an increasing diversity of *Nilssonia*. The ferns *Cladophlebis* and *Coniopteris* are, however, rarer. The assemblage appears to be of early Middle Jurassic age, though slightly younger than the Boroldaisky assemblage.

Higher in the Middle Jurassic section lies a Kashkaratinsky suite (not shown in Appendix), exposed in the valley of the Kashkaraty river (text-fig. 2, locality 11). This contains fragments of a typically Middle Jurassic assemblage, similar to floras of that age described from South Fergana (Brick 1935; Vakhrameev 1964, 1969; Gomolitsky 1972) and the Embensky region (Baranova and Kirichova 1972).

The Lower Jurassic (Upper Liassic) to Middle Jurassic floras of the Karatau Range resemble those of the Middle Asian province of the Indo-European palaeofloristic area. They include species not known beyond that province (e.g. *Nilssonia serrata*, *Taeniopteris ferganensis*), others known only in that province (*Cladophlebis magnifolia*, *C. suluctensis*, and *C. czopakensis*), and conifers found only in the

Indo-European area (*Storgaardia spectabilis*, *Ferganiella latifolia*, and *F. lanceolata*). But at the same time, the Karatau floras of this age differ from the southern floras of the Middle Asian province in showing fewer typically southern elements. Neither the Matoniaceae nor the Marattiaceae have been found, and only one species of the Dipteridaceae (*Clathropteris obovata*). The cycadophytes are not varied at specific or generic level, and the southern genera *Ptilophyllum*, *Otozamites*, and *Zamites* have not yet appeared. The Ginkgoales and Czekanowskiales are, however, rich and varied.

Sixtel (1954) and Vakhrameev (1964, 1970) observed differences in the composition of floras within the Middle Asian province of the Indo-European area—mainly that the number of species of cycadophytes diminished while moving northwards, with a simultaneous increase of Ginkgoales and Czekanowskiales. These features are shown by the Lower–Middle Jurassic floras of the Karatau Range located in the northern part of the Middle Asian province (northern subprovince), the Lower–Middle Jurassic floras of the intermontane depression of North Kirghizia, and of the basin of the Issyk-Kul Lake, Angren, Kok-Yangak. The differences between the two floras are probably due to the fact that the floras in the northern subprovince were isolated by mountains from the warm southern seas and lived in a colder and more continental climate.

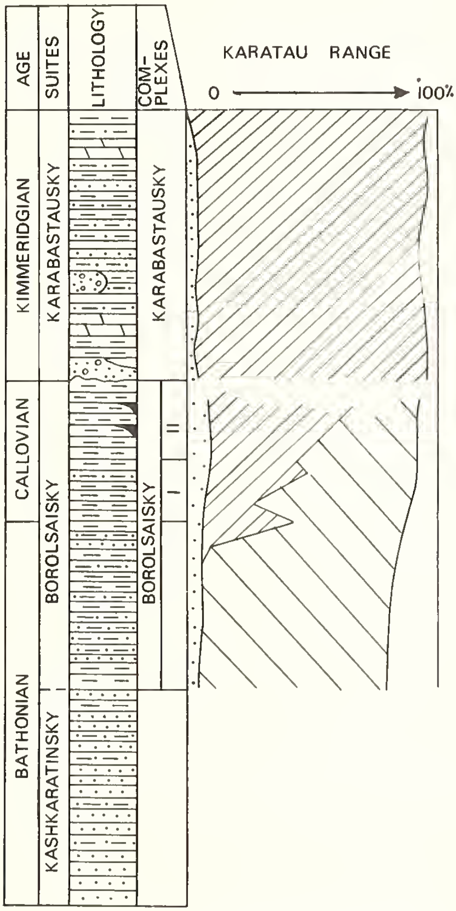
The Borolsaisky assemblage. This is the earlier of the two Upper Jurassic floras of the Karatau. It was collected in the vicinity of Chokhai (text-fig. 2, locality 12) in deposits of the Borolsaisky suite represented by claystones, siltstones, and combustible shales. These contain small fragments of leaves and shoots, with abundant plant detritus. The specimens are poorly preserved, cuticles are rarely present, and all the plants show signs of having been transported. The Appendix shows the composition of the flora according to the data of Turutanova-Ketova (1950, 1963; Problems of paleontology, 1963), Orlovskaya (1968, 1971), and on the basis of new samples collected by Doludenko. Turutanova-Ketova assigned this flora to the Middle Jurassic. However, because there are no equisetaleans and very few ferns, but a large number of conifers and cycadophytes, we consider that the flora is of Late Jurassic age.

The Karabastausky assemblage. This, the second Upper Jurassic flora, was collected in deposits of the Karabastausky suite of the Aulie area (text-fig. 2, locality 13). Specimens have been found near Chugurchak, Karabastau, and near the village of Uspenskoie (formerly Galkino) (text-fig. 2, localities 7, 8, 15). The Karabastausky suite is represented by thinly laminated carbonate rocks which contain an exceptionally rich and diverse flora and fauna. These sediments were deposited in the Upper Jurassic lake studied by Gekker (1948). Large, very well-preserved leaves of bennettitaleans and cycads, over 50 cm long, and large branches of conifers are common. The phytolema of many leaves is preserved, especially those of the conifers *Brachyphyllum* and *Pagiophyllum*, and we were able to extract spores from sporangia of *Stachypteris* and *Coniopteris*.

The Karabastausky flora is typical of the Upper Jurassic, having extremely few equisetaleans and ferns, but these include *Stachypteris*. It abounds in Bennettitales, especially *Ptilophyllum* and *Otozamites*, while cycads and the conifers *Brachyphyllum* and *Pagiophyllum* are prevalent. The Karabastausky flora is most similar in aspect to the Upper Jurassic floras of Georgia (Doludenko and Svanidze 1968, 1969), the Gissarian Range (Luchnikov 1972), and France (Saporta 1873, 1875, 1884, 1891; Lemoigne and Thierry 1968; Barale 1970; Borale, Cariou and Radureau 1974).

Miospores of the Upper Jurassic floras and their ages

The study of spore-pollen spectra from Jurassic deposits of the Karatau carried out during recent years by Vakhrameev and Yaroshenko (1958), Murakhovskaya (1968), and to a greater extent Sakulina (1968, 1971) enable us to determine the ages of the above two Upper Jurassic floras more precisely.



TEXT-FIG. 4. Diagram showing the distribution of *Classopollis* and of certain other miospores (after Sakulina 1971). *Right*, composition of pollen assemblages; dotted area represents percentage made up of spores, fine hatching indicates percentage made up of *Classopollis* pollen, coarse hatching indicates percentage made up of *Disaccites* pollen. Conglomerates, sandstones, etc., shown as in text-fig. 3.

The spore-pollen assemblages from the upper part of the Borolsaisky suite in the vicinity of Chokhai have been described by Sakulina (1968, 1971), who has recognized two subassemblages of miospores (text-fig. 4). The earlier subassemblage is characterized by the prevalence of disaccate pollen *Disaccites*, and the presence of a large amount of *Classopollis* pollen. The amount of *Classopollis* is negligible at first (0–2%), then gradually increases to 10–14%, jumps to 50%, and finally decreases to 10–20%. There are few species of *Classopollis* (mostly *C. classoides* and *C. minor*). Spores make up only 5–8% of this assemblage, rarely as much as 15%. The later subassemblage is characterized by an increased amount of *Classopollis* (38–58%) and a decreased amount of disaccate pollen; not more than 8% is made up of spores.

Sakulina (1971) surveyed the spore-pollen assemblages from the Bathonian–Tithonian deposits of Mangyshlak, western Uzbekistan, and the Karatau. She shows that those assemblages from the Early and Middle Callovian contain a lower content of *Classopollis* pollen (up to 50%, less frequently 70%) than those from the Upper Callovian–Tithonian. These comparative studies of miospore assemblages help in estimating the age of the Borolsaisky and Karabastausky assemblages. They indicate that the two miospore subassemblages from the Borolsaisky suite are probably of Early to Middle Callovian age.

Classopollis pollen is produced by members of the conifer family Cheirolepidiaceae, as are the shoots known as *Brachyphyllum* and *Pagiophyllum.* Vakhrameev (1970) has shown that the relative abundance of these elements of the floras can be used to define three climatic belts of latitude within the U.S.S.R. and adjoining regions, during the Bathonian, Late Jurassic, and Valanginian. The most southerly of these belts covers Moldavia, the Dnieper–Donets depression, Donets Basin, Crimea, Caucasus, Middle Asia, and Kazakhstan (including the Karatau region). In these regions there was, during the Bathonian, a notable decrease in the amount of *Classopollis* pollen (often of 15% and sometimes of 40%). In the Callovian, especially in the late Callovian, there was an increase in *Classopollis* to 60–75%, with a decrease in the percentage of spores of ferns and pine-like pollen. In the Oxfordian and Tithonian the amount of *Classopollis* pollen reaches 80–85% and sometimes even 95–100%.

Comparison of the composition of these two miospore subassemblages with those surveyed by Sakulina (1971), mentioned above, shows that they are characteristic of those from Lower and Middle Callovian times.

The spore-pollen assemblage of the Karabastausky suite has been studied by Murakhovskaya (1968) and Sakulina (1968, 1971). *Classopollis* pollen forms 95–100% of the assemblage throughout. The species of *Classopollis* are *C. classoides*, *C. pfluggii*, *C. intunensis*, *C. minor*, and *C. gyroflexus.* The amount of disaccate pollen *Disaccites* decreases to 2%. In the Karabastausky suite there occur *Perinopollenites*, *Foveoinaperturites*, *Ginkgocycadophytus*, *Inaperturopollenites*, *Araucariacites*, and *Caytonipollenites.* The spore *Cyathidites australis* predominates, while the following are sporadic: *Gleicheniidites*, *Sphagnumsporites*, *Lygodiumsporites*, *Concavisporites*, *Apiculatisporites*, *Tripartina variabilis*, *Laevigatosporites ovatus*, and *Ciborium junctum.*

Sakulina (1971) considers that assemblages similar to those found in the Karabastausky suite have been found in sediments of a wide range of ages, from Late Callovian to Kimmeridgian. Since no distinct series of miospore assemblages for this period of time have yet been recognized, this approach does not help in providing a more precise age for the Karabastausky deposits or flora. It is clearly, of course, later than the Borolsaisky deposits and assemblages, but the length of any gap in time between the two is unknown.

In summary, the plant macro-fossils and miospores both suggest a Late Jurassic age for the Borolsaisky and Karabastausky suites, while the miospores indicate, more precisely, that the Borolsaisky belongs to the Lower–Middle Callovian.

GENERAL DISCUSSION

A thorough study of floras growing in the restricted Karatau area during the Jurassic enables us to follow how the flora changed with age, climate, and the palaeogeographical environment. An analysis of the generic composition of the Jurassic flora of the Karatau suggests the following picture (Table 1).

The genera common in Lower, Middle, and Upper Jurassic deposits of the Karatau are as follows: *Equisetum*; ferns: *Clathropteris*, *Coniopteris*, *Cladophlebis*; cycadophytes: *Anomozamites*, *Pterophyllum*, *Williamsonia*, *Williamsoniella*, *Nilssonia*, *Pseudoctenis*, *Taeniopteris*; Ginkgoales and Czekanowskiales: *Ginkgoites*, *Sphenobaiera*, *Eretmophyllum*, *Czekanowskia*, *Phoenicopsis*; conifers: *Storgaardia*, *Podoza-*

TABLE 1. The generic composition of the Lower, Middle, and Upper Jurassic floras of the Karatau region. Columns Ku, Ak, Bd, Is, Bs, and Ka represent the Kurkureusky, Akbulaksky, Boroldaisky, Issyktasky, Borolsaisky, and Karabastausky floras, respectively. The numbers indicate the number of species of each genus in each flora.

		Ku	Ak	Bd	Is	Bs	Ka
ARTHROPSIDA	*Annulariopsis*	1					
	Neocalamites	1	2	1	1		
	Equisetum	1	1	2	2		1
FILICES	*Coniopteris*	2	2	3	1		3
	Sphenopteris						2
	Cladophlebis	6	6	10	3	1	1
	Clathropteris	1	1	1			1
	Raphaelia			2			
	Hausmannia						1
	Stachypteris						1
CAYTONIALES	*Sagenopteris*					1	1
BENETTITALES	*Nilssoniopteris*	1		2			
	Williamsoniella	1				2	1
	Anomozamites		6	2		1	
	Pterophyllum		2			1	1
	Williamsonia			1		1	
	Otozamites					1	5
	Ptilophyllum						1
	Zamiophyllum						1
	Zamites						1
	Sphenozamites						1
	Weltrichia						1
CYCADALES and unplaced CYCADOPHYTA	*Nilssonia*	1	1	2	3	1	3
	Pseudoctenis	2			1	1	
	Paracycas						1
	Taeniopteris	1	3	2	1		1
	Cycadites						2
GINKGOALES	*Ginkgoites*	2	2	2	1		1
	Baiera	1					1
	Sphenobaiera	1		1	1		2
	Pseudotorellia		1		2		
	Eretmophyllum			1			1
CZEKANOWSKIALES	*Czekanowskia*		1	3		1	1
	Phoenicopsis	1		2	2		1
CONIFERALES	*Storgaardia*	1				1	1
	Pityophyllum	2	2	2	1	2	1
	Podozamites		2	1			1
	Ferganiella		1	3			
	Elatocladus			1		1	3
	Pagiophyllum				1	1	5
	Brachyphyllum					1	5
	Araucarites						1

mites, *Pityophyllum*, *Elatocladus*, and *Pagiophyllum*. However, though most of these genera abound in the Lower and Middle Jurassic deposits, by the Upper Jurassic they are usually less numerous or even sporadic. A few genera are more restricted in their appearance in the Lower and Middle Jurassic. *Annulariopsis* is found only in the lower parts of the upper Lower Jurassic. The fern *Raphaelia* occurs only in the Middle Jurassic, and the conifer *Ferganiella* is known only in the upper part of the Lower Jurassic and the lower part of the Middle Jurassic. A number of genera, absent from earlier Karatau deposits, thus appear there in the Upper Jurassic, for the first time, as follows: *Hausmannia*, *Stachypteris*, *Sagenopteris*, *Otozamites*, *Ptilophyllum*, *Zamiophyllum*, *Zamites*, *Sphenozamites*, *Weltrichia*, *Paracycas*, and *Cycadites*, as well as conifers: *Araucarites*, *Brachyphyllum*, and *Pagiophyllum*, only the last being known in the uppermost parts of the Middle Jurassic. Many of these (*Ptilophyllum*, *Otozamites*, *Brachyphyllum*, *Pagiophyllum*, etc.) migrated to the Karatau from more southern regions and rapidly became predominant there.

The Karatau flora underwent significant changes during the 30–35 million years of its existence, these being especially pronounced in the Late Jurassic.

The early Middle Jurassic flora of the Karatau with taphocoenoses of the usual Kazakhstan Jurassic composition, consists of equisetaleans, ferns (*Clathropteris*, *Cladophlebis*, and *Coniopteris*), typical Jurassic Ginkgoales and Czekanowskiales, relatively uniform cycadophytes (*Anomozamites*, *Nilssoniopteris*, *Nilssonia*, *Pseudoctenis*, and *Taeniopteris*), and conifers; along with the widespread *Pityophyllum* and *Podozamites*, the broad-leaved *Ferganiella* is numerous. This flora gives way to a new type of flora resembling the Upper Jurassic floras of France and Georgia, characterized by the predominance of Bennettitales (Ptilophyllum, Otozamites) and conifers of the *Brachyphyllum–Pagiophyllum* type, a small number of ferns and Ginkgoales, and only occasional equisetaleans.

The floral changes of the Karatau region during the Jurassic can be related to alterations in the palaeogeographical conditions and climate. In Early to Middle Jurassic times, the Karatau deposits appear to have accumulated in an alluvial plain with numerous rivers with oxbows. We picture the climate as warm and humid, permitting the vigorous growth of a rich vegetation that covered the banks of the rivers and, no doubt, the higher ground also. Huge masses of dead plants, later to form coal, accumulated in the swamps.

In the Late Jurassic a very large lake formed in place of the alluvial plain. This was called Lake Karatausky by Gekker (1948), but Buvalkin (1968) named it Lake Karabastausky. It was a mountain lake with rocky banks, its water containing great amounts of calcium and magnesium salts. The banks of the lake and of the rivers flowing into it were covered by rather rich vegetation. When judged by the composition and structure of the plants, the Karatau climate of this time was dry and hot. Lake Karatausky was in the belt of arid climate that appeared in the Late Jurassic within the Indo-European palaeofloristic area, stretching from the western boundary of Spain and France via South Europe, the Caucasus, Kazakhstan, and the Middle Asian province to Central China. Such a climatic change from a humid Early and Middle Jurassic and an arid Late Jurassic was suggested by Strakhov (1960), and would certainly have affected the composition of the Karatau flora.

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APPENDIX

Comparison of the specific composition of Early, Middle, and Late Jurassic floras of the Karatau (from the data of Brick (1925*a–c*), Orlovskaya (1968, 1971), Prinada (*in* Buvalkin, 1958), Romanova (1961), Turutanova-Ketova (1929, 1930, 1936*a*, *b*, 1950, 1963), The principles of palaeontology (1963), Gekker (1948), and the authors).

The detailed composition of each flora is given in turn. Each taxon is listed under the *first* flora in which it occurs. If any taxon also occurs in a later flora, this is shown as a number after its name, as follows: 1, Akbulaksky assemblage; 2, Boroldaisky assemblage; 3, Issyktasky assemblage; 4, Borolsaisky assemblage; 5, Karabastausky assemblage.

Lower Jurassic Kurkureusky flora:

Annulariopsis inopinata, *Neocalamites issykkulensis*, *Equisetum* ex gr. *gracilis*, *Clathropteris obovata* (1), *Coniopteris zindanensis*, *Coniopteris* sp. (1–3), *Cladophlebis denticulata* (1–3), *C. nebbensis* (1–3), *C. whitbiensis* var. punctata (1, 2), *C. czokpakensis*, *C. haiburnensis* (1–3), *C. magnifolia* (1, 2), *Nilssoniopteris karataviensis*, *Williamsoniella vachrameevii*, *Nilssonia acuminata* (1–3), *Pseudoctenis locusta*, *Taeniopteris* sp. A, *Ginkgoites* ex gr. *sibiricus* (2, 3, 5), *Baiera* cf. *gracilis*, *Sphenobaiera* sp., *Phoenicopsis* ex gr. *angustifolia* (2, 3, 5), *Storgaardia spectabilis*, *Pityophyllum angustifolium* (1, 2, 4), *P.* ex gr. *nordenskioldii* (1–4), *Pityocladus kobukensis* (1, 3), *Stenorhachis dubius*, *Carpolithes heeri*.

Lower Jurassic Akbulaksky flora:

Neocalamites hoerensis, *Neocalamites* sp. (2, 3), *Equisetum laterale* (2, 3, 5), *Coniopteris* ex gr. *hymenophylloides* (2, 5), *Cladophlebis suluktensis* (2), *Anomozamites lindleyanus*, *A. dentatus*, *A. elegans*, *A.* ex gr. *inconstans*, *A.* cf. *lockyi*, *Anomozamites* sp. (4), *Pterophyllum* cf. *tietzei*, *Pterophyllum* sp. (4, 5), *Taeniopteris ferganensis* (2), *T.* ex gr. *amurensis*, *Ginkgoites* sp. A, *Pseudotorellia* sp. (2, 3), *Czekanowskia rigida* (2), *Podozamites lanceolatus* (2, 5), *P.* cf. *latifolius*, *Ferganiella ovalis* (2).

Middle Jurassic Boroldaisky flora:

Marchantites baicalensis, *Lycopodites trichiatus*, *Equisetum hallei*, *Clathropteris* sp. (5), *Cladophlebis bidentata*, *C. argutula*, *C. kamenkensis*, *C.* aff. *magnifica*, *Raphaelia diamensis* forma *spinosa*, *R. dentata*, *Nilssoniopteris* aff. *vittata*, *N. boroldaica*, *Anomozamites kornilovae*, *Williamsonia haydenii*, *Nilssonia* sp. (3, 4), *Taeniopteris ensis*, *Ginkgoites* sp. B, *Eretmophyllum boroldaica*, *Sphenobaiera longifolia*, *Phoenicopsis* ex gr. *rarinervis*, *Czekanowskia ketovae*, *Czekanowskia* sp. (4), *Ixostrobus heeri* (3), *Elatocladus conferta*, *Ferganiella lanceolata*, *F. latifolia*.

Middle Jurassic Issyktasky flora:

Thallites sp., *Equisetum* cf. *beanii*, *Equisetum* sp., *Nilssonia serrata*, *Taeniopteris* sp. (5), *Sphenobaiera* sp. B, *Pseudotorellia ephela*, *Phoenicopsis* ex gr. *speciosa*, *Pagiophyllum setosum* (4).

Upper Jurassic Borolsaisky flora:

Cladophlebis sp. (5), *Sagenopteris phillipsii* (5), *Williamsoniella karataviensis* (5), *W. czochaiensis*, *Williamsoniella* sp., *Williamsonia* sp., *Otozamites* sp., *Brachyphyllum* sp., *Elatocladus ketovae*, *Elatocladus* sp., *Taxocladus*? sp., *Storgaardia* sp,, *Pityspermum crassialigerum*, *P. cuneatum*, *P. falciforme* (5), *P. gracile* (5), *P. karataviense* (5), *P. lacum* (5), *P. lundgrenii* (5), *P. maakiana* (5), *P. nansenii* (5), *P. obliquum* (5), *P. parallelimarginale*, *P. pinisimulans*, *Pityostrobus* sp. (5), *Machairostrobus kazachstanicus*, *Masculostrobus* sp., *Carpolithes heeri*, *C. karatavicus*, *C. cinctus*, *Platylepidium oblanceolatum* (5), *P. leve* (5), *P. minus*, *Samaropsis rotundata*, *S. problematica*, *S. kazachstanica*, *Stenomiscus magnus*.

Upper Jurassic Karabastausky flora:

Marchantites sp., *Stachypteris turkestanica*, *Coniopteris angustiloba*, *C. murrayana*, *Sphenopteris modesta*, *S.* cf. *moissenetii*, *Hausmannia* sp., *Weltrichia auliensis*, *Ptilophyllum caucasicum*, *Otozamites turkestanicus*, *O. hislopii*, *O. latior*, *O. giganteus*, *O.* cf. *beanii*, *Sphenozamites sphenozamioides*, *Zamiophyllum buchianum*, *Zamites*? sp., *Cycadolepis* sp., *Paracycas harrisii*, *Nilssonia* aff. *obtusa*, *N.* ex gr. *orientalis*, *Cycadites dubius*, *C. saportae*, *Baiera colchica*, *Sphenobaiera kazachstanica*, *S. spectabilis*, *Eretmophyllum magnum*, *Czekanowskia auliensis*, *Desmiophyllum* sp., *Araucarites vassilevskae*, *Brachyphyllum mamillare*, *B. expansum*, *B. expansum* var. *gracilis*, *B. expansum* var. *falcata*, *B. mamillareforme*, *B. gracile*, *B. brickae*, *Pagiophyllum peregrinum*, *P. papillatum*, *P. ketovae*, *P.* cf. *burmense*, *P. falcatum*, *Pagiophyllum* sp., *Elatocladus jabalpurensis*, *E. minutus*, *E. subzamioides*, *Storgaardia kazachstanica*, *Podozamites angustifolius*, *Pityophyllum* sp., *Pityospermum cedriformis*, *Conites* sp., *Carpolithes karatavicus*, *Problematospermum ovale*, *P. elongatum*.

SILICONE RUBBER CASTS OF SILICIFIED PLANTS FROM THE CRETACEOUS OF SUDAN

by JOAN WATSON *and* K. L. ALVIN

ABSTRACT. Silicified plant fragments, including the conifer *Frenelopsis* from the Lower Cretaceous of Sudan, are preserved as internal and external moulds. Low viscosity silicone rubber has been used to obtain casts showing fine details which may be studied by scanning electron microscopy.

WORK in progress on a revision of conifers belonging to the genus *Frenelopsis* Schenk has led us to re-examine some silicified material from the Nubian Sandstone of Eastern Darfur, Sudan. The material, which is in the collection of the British Museum (Natural History), was studied by Edwards (1926) and includes some shoots which he described and figured as *F. hoheneggeri* (Ettingshausen). The plants are entirely replaced by silica, none of the original plant material remaining. In the absence of a cuticle, we tried to obtain rubber impressions for use in the scanning electron microscope. The results obtained revealed exquisite details and showed the preservation to be of a most unusual and interesting kind. The taxonomy and morphology will be dealt with elsewhere. The purpose of this paper is to demonstrate our replica technique in conjunction with this unusual and exceptionally fine preservation.

MATERIAL

The matrix is a silicified grit of highly variable grain size. There are nine pieces in the collection, some from loose weathered blocks, others collected *in situ*. Few details are given by Edwards (1926) about the geological occurrence of the specimens but the reported discussion following the original reading of his paper indicates that they occur in association with 'soda-rich volcanic rocks' of later age. One of the specimens (B.M. (N.H.) V.21708) is shown in Plate 96, fig. 1 at natural size.

Besides the *Frenelopsis* shoots there are cone remains, pieces of wood, and fragments of the fern *Weichselia reticulata* (Stokes and Webb). At first sight the shoots on the weathered surface appear to show certain details of the external surface of the leaves and internodes, such as rows of stomata and cell outlines, and these were figured by Edwards (1926, p. 96, fig. 4) using line drawings. However, when a piece of shoot from the rather crumbly unweathered material is mounted and examined under the SEM the result is rather surprising (Pl. 97, figs. 1 and 2). Clearly this is not the external surface of the shoot but silica infillings of the cells of the epidermis with gaps where the cell walls were. It can be seen in Plate 97, fig. 3 that the silica is in the form of euhedral quartz crystals up to about 10 μm in length.

METHODS

We obtained casts of the exposed plant surfaces using a low-viscosity silicone rubber. The rubber, called 'Silflo', is a two-part impression material used in dentistry and

[Palaeontology, Vol. 19, Part 4, 1976, pp. 641–650, pls. 96–99.]

made by Flexico Developments Ltd. It is extremely easy and quick to use and the few problems which arise are easily overcome. The rubber is quickly mixed with its catalyst on a tile by means of a small spatula and then scooped onto the required area, again working fairly quickly. The rubber is white and the catalyst either colourless or dyed green; the green is preferred as it is much easier to see when mixing is complete. The amount of catalyst to use must be established by trial and error as it tends to deteriorate with age. Too much causes the rubber to start setting before it is put onto the rock surface and this results in loss of detail in the cast. Another result of too much catalyst is that it can come to the surface of the specimen during coating for the SEM and the gold mixes with it to form a sludge. We recommend always leaving the rubber impressions for twenty-four hours before coating, to ensure that the catalyst has entirely evaporated.

There is little trouble with air bubbles as they mostly rise to the surface quite quickly. However, in a particularly cavernous specimen such as the cone in Plate 99, fig. 1 gentle poking of the liquid rubber in the cavities with a needle helps the process.

We usually prefer to discard the first cast taken from a particular area, using it as a method of cleaning the surface. It is most satisfactory to work with small areas at a time; usually 1 cm^2 is sufficient for a SEM mount. Larger casts can be built up with several batches of freshly mixed Silflo as it bonds to itself completely. Such a large cast is shown in Plate 96, fig. 2, coated with aluminium to increase contrast. For SEM work there is the problem of sticking the smooth shiny surface to the metal stub. This was overcome by pressing a scrap of filter paper onto the surface of the unset rubber. The resulting specimen is easily cut to size with scissors and mounted by means of double-sided 'Sellotape'. The specimens were mostly coated with gold using a 'Rota Cota', but high relief specimens such as the cone-scale (Pl. 99, fig. 3) required sputter coating for satisfactory results.

The only other minor problem encountered is that sometimes the rubber has a finely wrinkled surface as shown in Plate 99, fig. 6. It is only detected at magnifications around ×2000 and does not seem to affect the useful detail but clearly we would prefer to eliminate it. It is certainly a feature of the Silflo, not the rock, as we have reproduced it in impressions of fingerprints, cardboard, and a wooden surface. However, we are not yet able consistently to reproduce or eliminate it.

EXPLANATION OF PLATE 96

All British Museum (Natural History) specimen numbers.

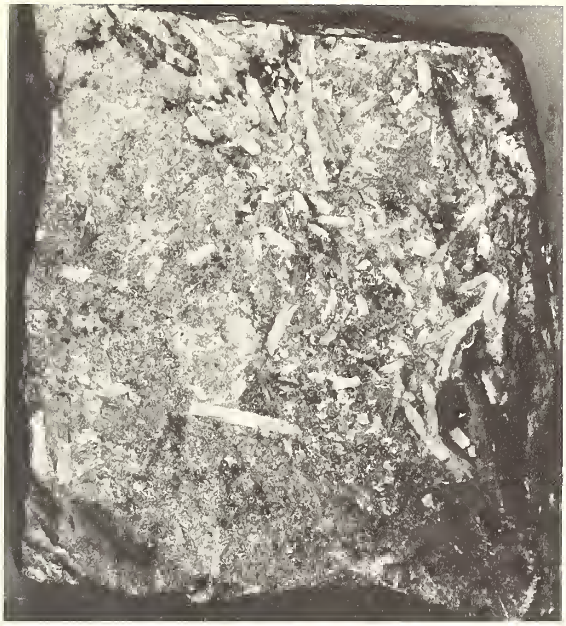
Fig. 1. Silicified specimen used to prepare several of the rubber casts figured in this paper, ×1. V.21708.

Fig. 2. Silicone rubber cast of *Frenelopsis* shoots, coated with aluminium to give good contrast, ×3. Prepared from the bottom right-hand corner of V.21708.

Fig. 3. SEM montage of silicone rubber cast of *Frenelopsis* shoot, ×15. Cast prepared from same area of V.21708 as fig. 2.

Fig. 4. SEM of silica specimen showing grit matrix on right and external mould of *Frenelopsis* on left, ×50. From V.21708.

Fig. 5. Transverse section of little flattened *Frenelopsis* shoot seen under crossed polars, showing cryptocrystalline silica replacing plant material and cementing detrital grains. Powdery silica replacement of cuticle does not survive sectioning and now shows as a gap between external mould and steinkern (black ring), ×50. Thin section taken from V.21708.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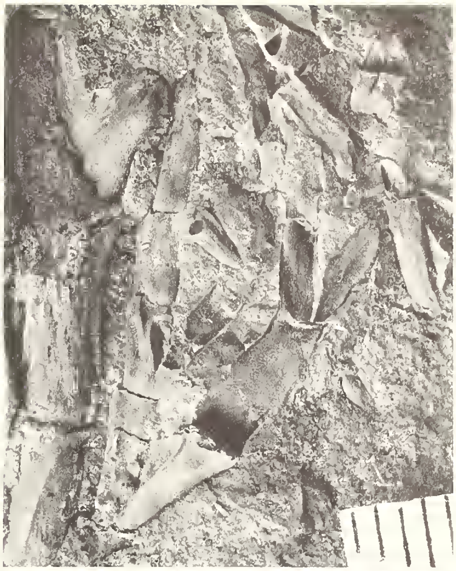
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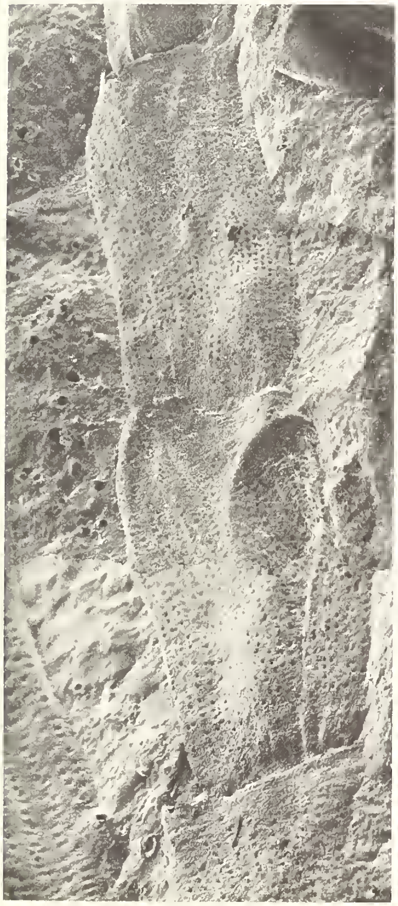
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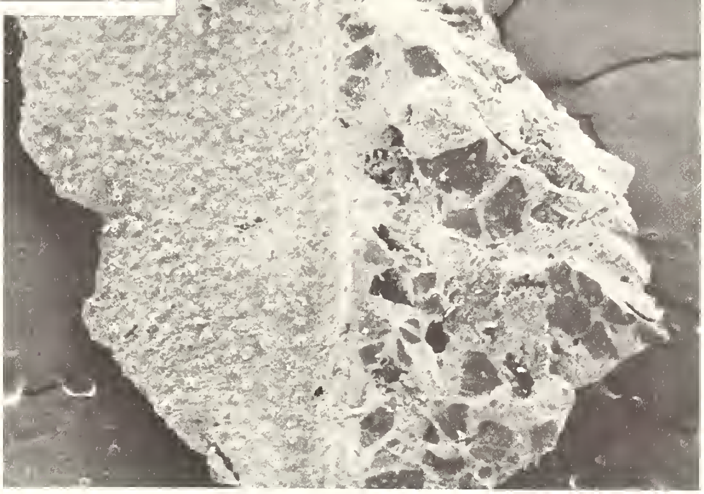
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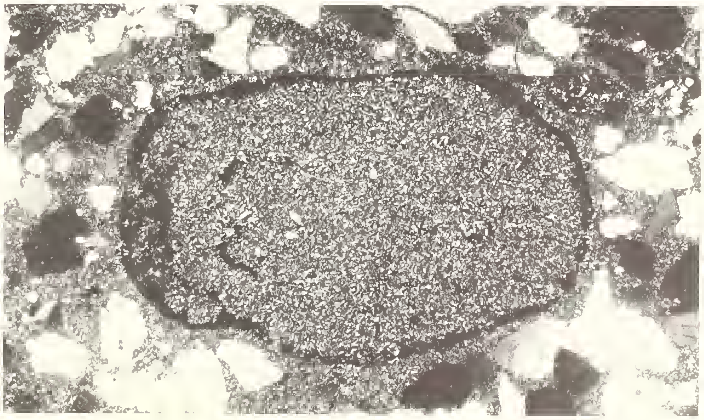
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WATSON and ALVIN, *Frenelopsis*

It should also be mentioned in relation to SEM studies that the thickness of the rubber specimen may produce too short a working distance and to avoid this it is advisable to use stubs with thin tops (galvanized roofing nails are perfectly adequate).

RESULTS

When a shoot surface such as shown in Plate 97, figs. 1–3 is used to obtain a rubber impression the result is as shown in Plate 97, figs. 5 and 6. This looks to us like a cast of the inner surface of the cuticle but may include additional portions of the anticlinal walls of the epidermis, possibly representing the cutinized parts of these walls. We have not seen guard cells in such an internal cast, possibly because they were too thinly cutinized.

A cast of the external surface of the shoot is obtained by taking an impression from the matrix in a place where the silica shoots have been removed as on the left-hand side of Plate 96, fig. 4. In contrast to the coarseness of the grit, with grains up to 1 cm across, the matrix immediately adjacent to each plant specimen is very fine grained and forms a crust which is a perfect external mould of the plant. All such surfaces show a pattern of protruberances (Pl. 98, fig. 1; Pl. 99, fig. 2) representing silica plugs which crystallized inside the stomatal pits and it is in specimens where these are intact that the finest details survive.

Thus, we have fine-grained silica moulds, both internal and external, of the outer part of the epidermis with a gap between them. This is a common enough situation with calcareous invertebrate fossils but in this case the cryptocrystalline silica has preserved details at the cellular level in both the steinkern and the external mould. The gap between the two is filled with a fine white powder (also crystalline silica) and can be seen on newly exposed surfaces but it does not survive handling or the making of a thin section. Thin sections (Pl. 96, fig. 5) show that the interstices between the detrital grains are filled with the same cryptocrystalline siliceous cement as that forming the internal and external moulds of the plants.

Text-fig. 1 is a diagrammatic representation of the state of preservation together with the relationships of the various surfaces of silica and Silflo. The reconstruction of the situation depicted in text-fig. 1 was greatly assisted when a portion of steinkern was pulled off partially embedded in the Silflo cast (Pl. 98, fig. 3). Thus where the Silflo has seeped into the gap between the two moulds we get an approximation to

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EXPLANATION OF PLATE 97

All scanning electron micrographs.

Fig. 1. Silica surface which forms internal mould of *Frenelopsis* cuticle, ×150. V.17224.

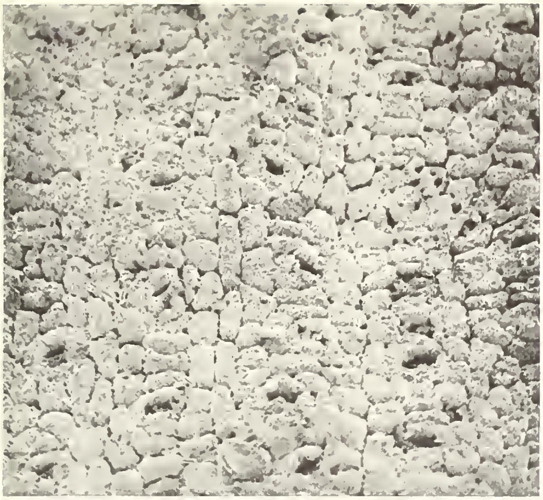
Fig. 2. Silica infillings of epidermal cell lumina, ×750. V.17224.

Fig. 3. Detail of same specimen as fig. 2 showing euhedral quartz crystals and gaps where cell walls were, ×3750.

Fig. 4. Silica infillings of tracheids and ray cells, ×150. V.21706.

Fig. 5. Silicone rubber cast taken from surface such as seen in fig. 1, ×100. Prepared from V.21708.

Fig. 6. Silicone rubber cast of internal surface of single stoma, ×500. V.21708.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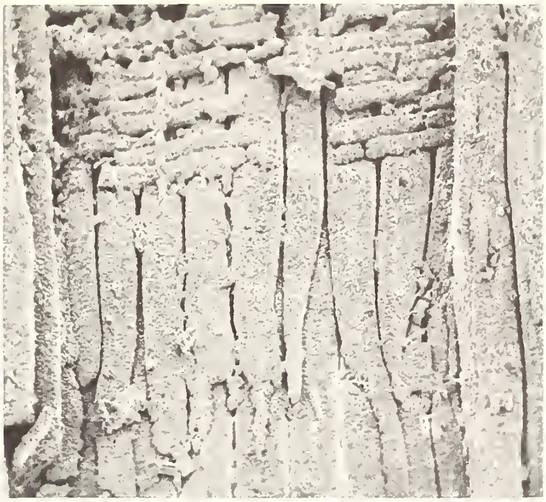
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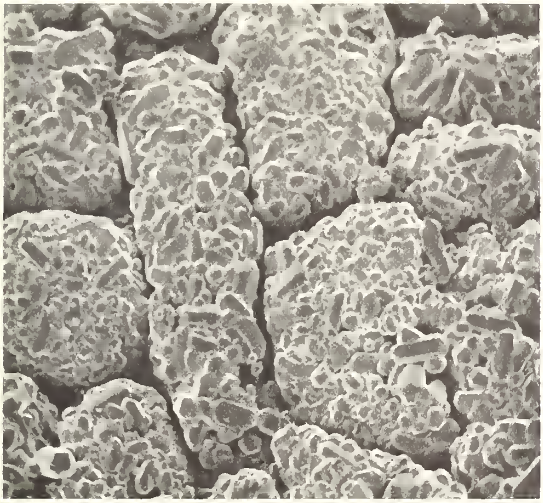
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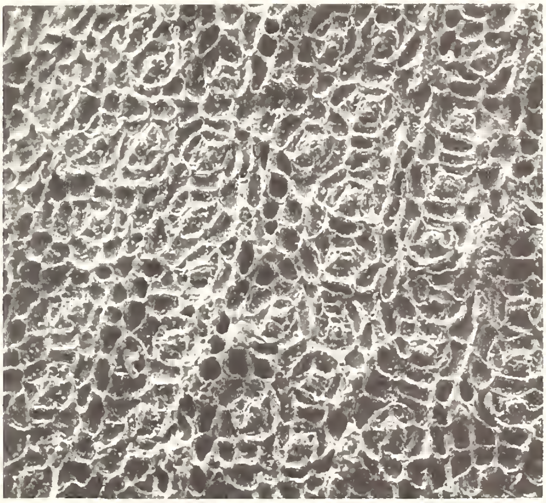
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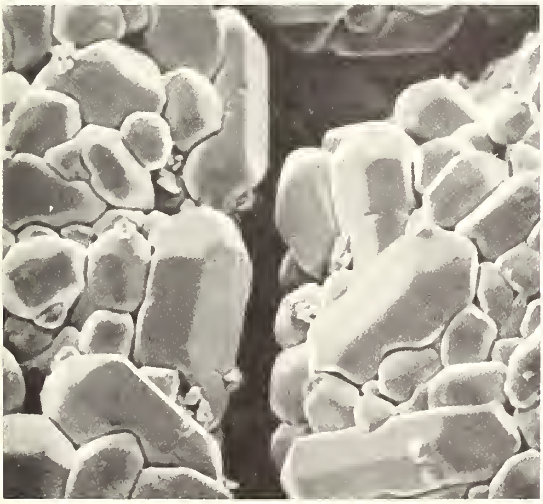
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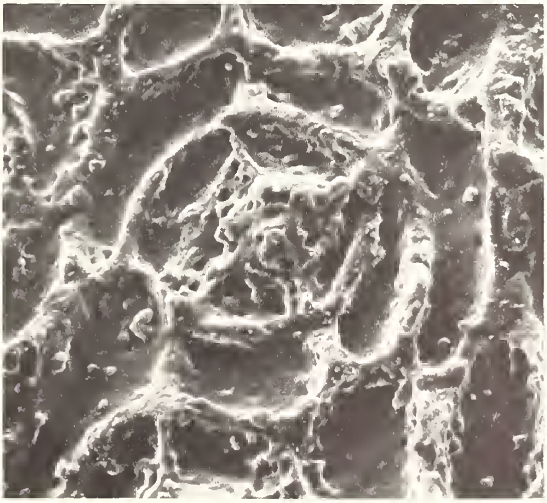
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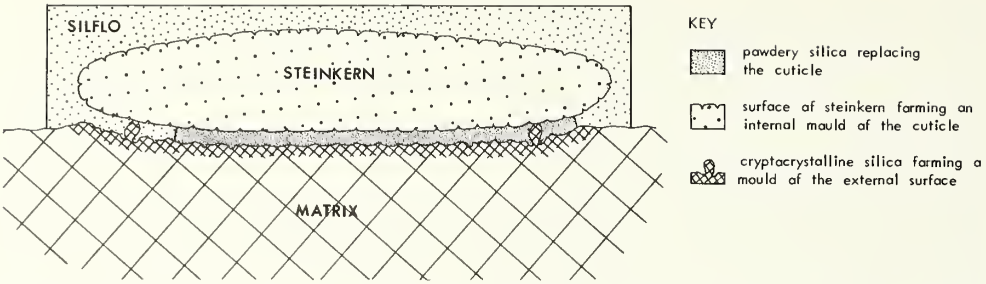
SILFLO
STEINKERN
MATRIX
KEY
powdery silica replacing the cuticle
surface of steinkern forming an internal mould of the cuticle
cryptocrystalline silica forming a mould of the external surface

TEXT-FIG. 1. Diagrammatic representation of transverse section of stem in relation to matrix and rubber casts.

the thickness of the cuticle (Pl. 98, fig. 2) disregarding any small degree of compression which may have occurred or additional cell wall material which may be represented.

The casts of the external surface show numerous fine details and several examples are shown in Plates 96, 98, and 99. Plate 98, fig. 4 shows the stomatal arrangement and the papillate surface of the epidermis; Plate 98, fig. 5 shows what might possibly be the upper surface of the guard cells and stomatal aperture; Plate 99, fig. 6 shows the stomatal pit and subsidiary cell papillae. All the *Frenelopsis* shoots appear to be preserved in exactly the same way.

The cones are preserved in an essentially similar manner to the shoots but in the one large cone the steinkerns of individual scales are all broken or missing. Thus there are only external moulds of silica which crystallized around all the scales, penetrating deeply between them. These moulds therefore give accurate casts of the original cone scales showing beautiful details of the surface including delicate hairs along the margin (Pl. 99, fig. 4).

The wood fragments present in the material are preserved somewhat differently, being represented by silica infillings of the cell lumina. Plate 97, fig. 4 shows infillings of tracheids with tapered ends and medullary ray cells, everywhere with gaps where the cell walls were. Edwards (1926) figured growth rings in the wood and a pattern of pitting in the tracheids. We examined the thin sections used by Edwards and found

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EXPLANATION OF PLATE 98

All scanning electron micrographs.

Fig. 1. Silica surface which forms external mould of *Frenelopsis* shoot showing protruberances which represent infillings of stomatal pits, ×750. V.21708.

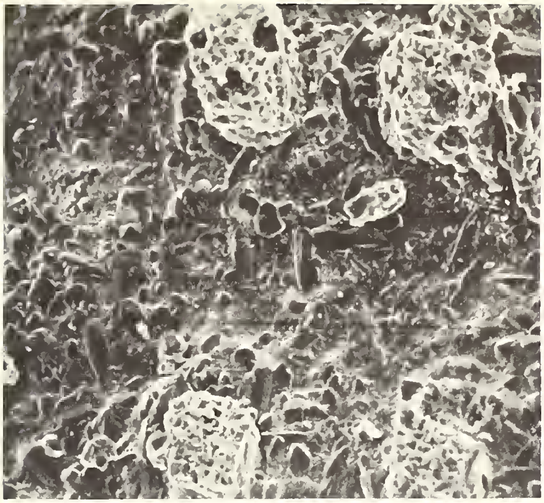
Fig. 2. Edge of rubber cast of *Frenelopsis* cuticle obtained when silicone rubber seeps between external mould and steinkern, ×750, tilted at 55°. V.17224.

Fig. 3. Steinkern of a *Frenelopsis* internode partially enclosed in silicone rubber impression; 'rubber cuticle' overlapping it is that shown in fig. 2, ×40. V.17224.

Fig. 4. Surface of rubber cast of *Frenelopsis* internode showing stomata and papillae, ×200. V.17224.

Fig. 5. Detail of specimen shown in fig. 4, ×500.

Fig. 6. Silica infillings of two tracheids showing pits, ×750. V.21706.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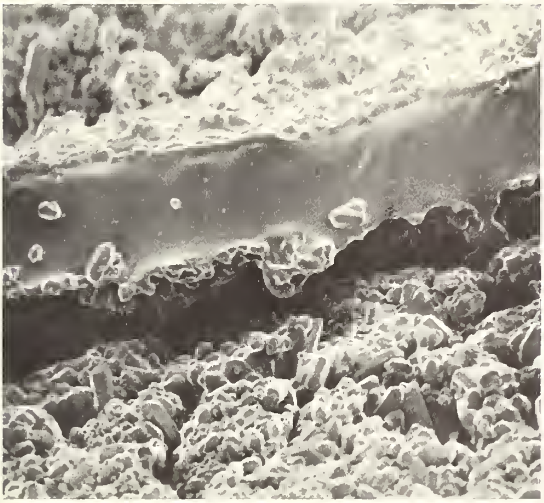
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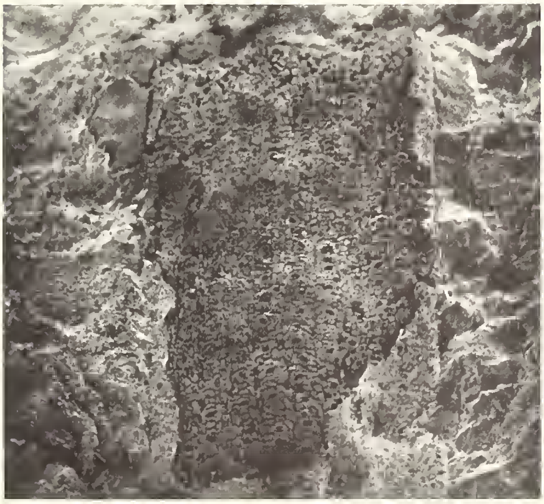
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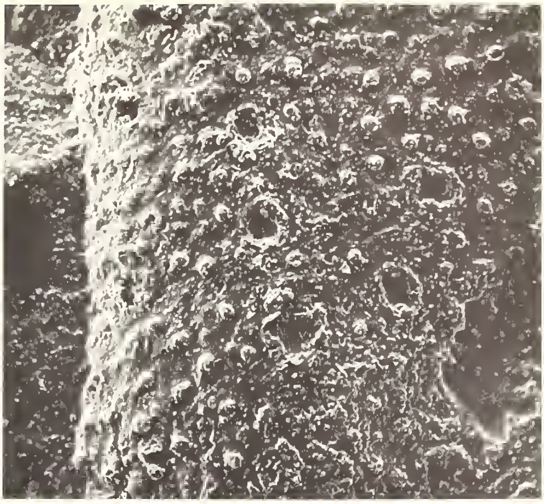
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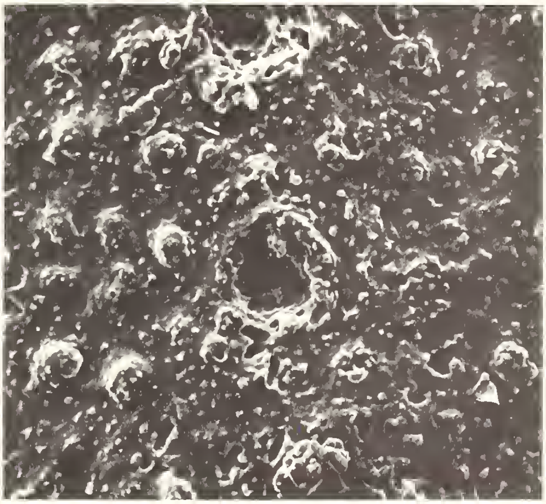
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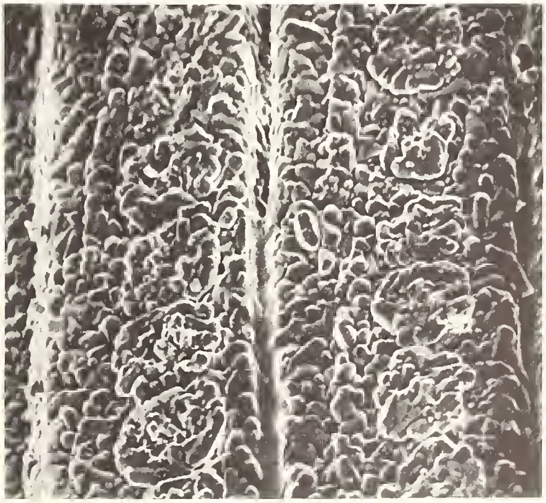
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WATSON and ALVIN, *Frenelopsis*

that both the cells and the pits are clearly outlined by 'Carborundum' (or other abrasive powder) filling the gaps mentioned above. We have also located pits with the SEM (Pl. 98, fig. 6) but the exact state of their preservation is unclear. They appear lens-shaped and we presume that each represents a silica infilling of the pit chambers of a pit pair attached to the infilling of one of the tracheids. However, we have been unable to find corresponding depressions in other tracheids.

DISCUSSION

The sequence of preservation can only be surmised but clearly in the case of the *Frenelopsis* shoots the fine-grained secondary silica, both internal and external, must have crystallized whilst the cuticle was still intact, the cuticle itself being removed at a later stage. We know, from our studies of compressed specimens of *Frenelopsis* from elsewhere, that the cuticle is often leathery and resistant, and it is easy to picture a stage in decay where the shoot consisted only of cylinders of cuticle, joined together at the nodes, trapped in the detrital matrix. Thin sections show detrital grains inside a few shoots. This would accord with a damaged cylinder of cuticle allowing entry of grains from the unconsolidated sediment before becoming entombed in the crystallizing secondary silica.

The use of low-viscosity silicone rubber casts of fossil plants for SEM studies has been briefly reported (Dilcher 1974) as has the use of latex rubber (Chaloner and Gay 1973). We find that Silflo has several distinct advantages over latex rubber. It is very quick to use; there is no water in the mixture and therefore no damage even to a clay matrix; there is no detectable shrinkage even over a period of months; air-bubble problems are reduced to a minimum.

Acknowledgements. The scanning electron microscopy was carried out partly on a Cambridge 'Stereoscan' in the Department of Textile Technology, University of Manchester Institute of Science and Technology, and partly on a similar instrument in the Department of Botany, Imperial College, London.

EXPLANATION OF PLATE 99

Fig. 1. Silica mould of female cone, ×5. V.21704.

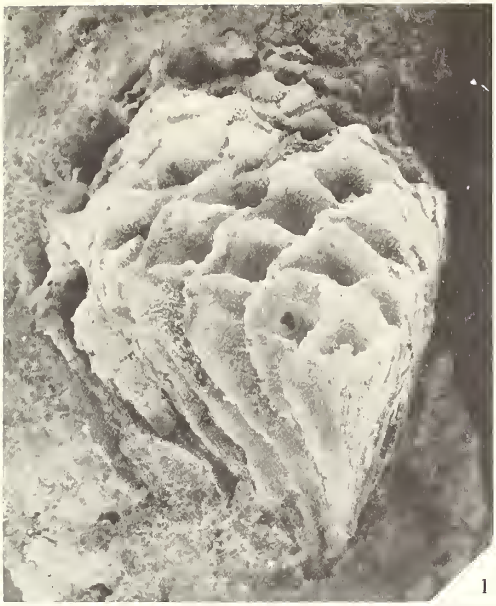
Fig. 2. External mould of single cone scale showing pegs which are infillings of stomatal pits, ×27. V.21704.

Fig. 3. Scanning electron micrograph of rubber cast of cone scale obtained from mould seen in figs. 1 and 2, ×40.

Fig. 4. Detail of same cone scale showing fringe of hairs on margin, ×80.

Fig. 5. Scanning electron micrograph of rubber cast of *Frenelopsis* internode surface. This is an example of specimens with wrinkled surface mentioned in text; wrinkling not detected at this low magnification (see fig. 6), ×225. Prepared from V.21708.

Fig. 6. Single stoma from specimen seen in fig. 5, showing well-preserved papillae; fine wrinkling seen at this higher magnification, ×2250.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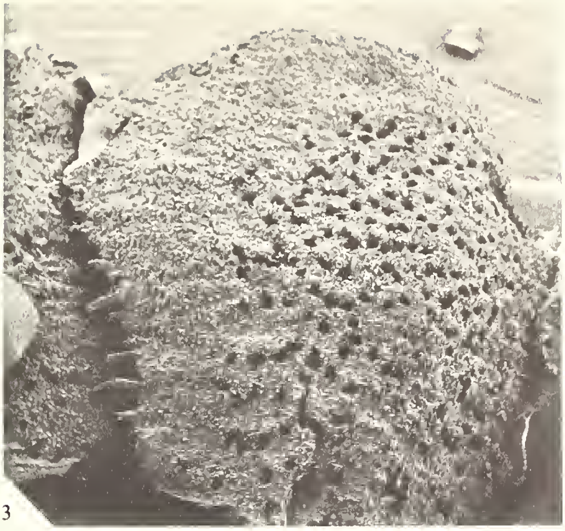
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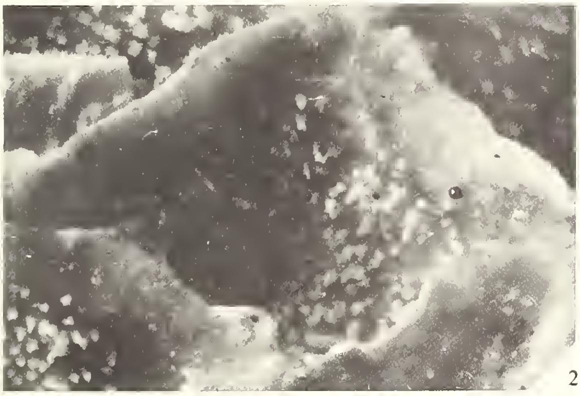
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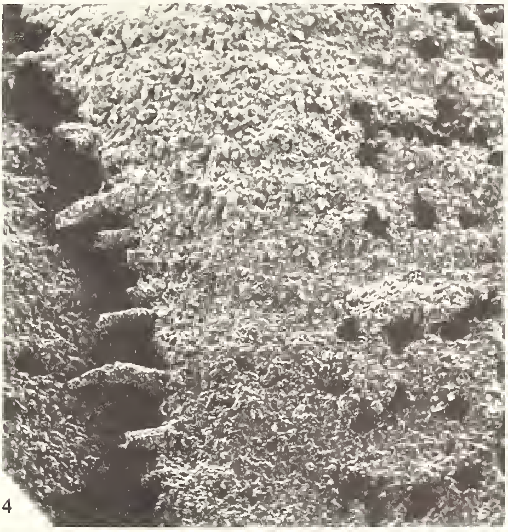
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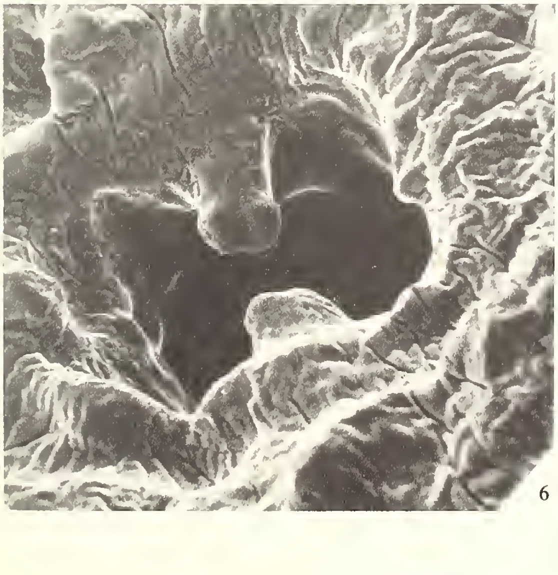
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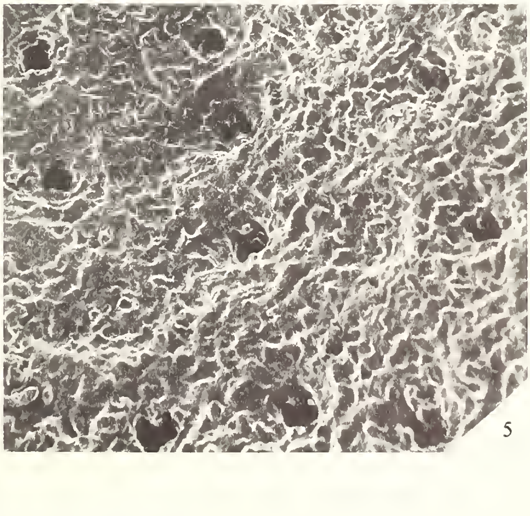
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WATSON and ALVIN, *Frenelopsis*

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PROMELOCRINUS FROM THE WENLOCK AT DUDLEY

by J. C. BROWER

ABSTRACT. Two melocrinitids occur in the Wenlock at Dudley. *Promelocrinus anglicus* Jaekel is represented by many specimens, whereas *Promelocrinus* sp. is only known from one partial fragment of the arms. Growth and variation have been studied in *P. anglicus*. Variation of number of plates in the interbrachial areas and in the ray trunks increases distally. The number of plates in a range of interbrachials is positively linked with the number of plates in adjacent ranges. However, the arm-branching parameters are mainly independent of one another. The earliest crinoids probably bear equal-sized arms in each ray with pinnules being present in the two outer arms but lacking in the two inner ones. Throughout subsequent development, the outer arms are unbranched although new brachials form and the length of the arms is augmented. The inner arms become hypertrophied into highly ramified ray trunks. The length of the ray trunk increases by the formation of new brachials and height increase of old plates. New ramules appear as new brachials are added to the ray trunk. Once the ramules are initiated, new brachials form at the distal tips of the growing ramules. Pinnules develop on the ramules and outer arms throughout growth. Lengths of old pinnules are augmented by the same mechanisms seen in the ramules and outer arms. The ontogeny of *P. anglicus* suggests that the acquisition of complexly ramified ray trunks results in unusually rapid rates of growth of new brachials and length of the arms. The rate of development is approximately squared relative to idealized crinoids with simple arm configurations. Unlike most crinoids, *P. anglicus* is characterized by isometry or positive allometry of the food-gathering system relative to tissue volume, so that the food-gathering ratios are either stabilized or increase throughout ontogeny. In *P. anglicus* and other melocrinitids, a complete filtration network is present which covers the entire perimeter of the arms, and almost all food particles flowing through the arms and pinnules would be filtered. Promelocrinids and melocrinitids were full mucus net feeders like most Recent adult crinoids.

MELOCRINITIDS and their allies represent one of the most diversified groups of Palaeozoic camerate crinoids, including about 120 species and subspecies, grouped in six genera. The evolution of melocrinitids has been described by Kirk (1929), Moore and Laudon (1943, pp. 89, 96–98), and Ubaghs (1953, pp. 710–712; 1958) and early forms were examined quantitatively by Brower (1973, pp. 432–437). The ancestral glyptocrinids are characterized by two unbranched arms in each ray and a filtration network with large gaps. The first step in evolution was the acquisition of four arms per ray. Subsequently, the inner arms of each ray became hypertrophied into highly ramified ray trunks while the outer arms were reduced and eventually lost in order to provide room for the ray trunks. This process increases the food-gathering capacity as well as forming a complete filtration net which completely filters the water in the vicinity of the crinoid. The general tendency is to increase the body size of adult crinoids throughout the lineage. The concomitant evolution of increased size and food-gathering capacity is suggestive of size-related allometry.

While engaged in a numerical study of the evolution of melocrinitids (Brower, in press) it was noticed that the British forms had never been fully described. Consequently the purpose of this paper is to present systematic descriptions of the melocrinitids from the Wenlock at Dudley, and in particular, to study growth and variation in *Promelocrinus anglicus* Jaekel.

[Palaeontology, Vol. 19, Part 4, 1976, pp. 651–680, pls. 100–102.]

TERMINOLOGY

Generally, the terminology follows that of Moore (1952, text-fig. 18-2). The proximal plate of the camerate *CD* (posterior) interray is designated primanal (Jaekel 1918, p. 28). Brachials rigidly incorporated into the calyx are termed fixed-brachials. The ray-orientation system is that of Carpenter (1884, text-fig. 2).

The camerate crinoids examined here have two to four free arms in each ray. Two-armed species show two half-rays; the area between these and the equivalent position in four-armed crinoids is termed an intersecundibrachial area, the calyx plates of which are intersecundibrachs. In four-armed taxa, two half-rays are present, each consisting of two free arms called quarter-rays. The space between two quarter-rays contains the intertertibrachs. All plates located between the rays are interbrachials. The camerate plate sequence directly overlying the primanal is the anal series, the elements of which are anal-series plates. The anal series is generally separated from the *C* and *D* rays by *CD* interray interbrachials.

Promelocrinids have four arms in each ray. The inner arms are hypertrophied into ray trunks which consist of uniserial nonpinnulate brachials. Pinnulate ramules are located along the ray trunks. The outer arms remain unbranched (see text-fig. 2*a* and *c* for illustration of terms).

SYSTEMATIC PALAEONTOLOGY

Subclass CAMERATA Wachsmuth and Springer, 1885
Order MONOBATHRIDA Moore and Laudon, 1943
Suborder GLYPTOCRININA Moore, 1952
Superfamily MELOCRINITICAE Ubaghs, 1953
Family MELOCRINITIDAE Zittel, 1878
PROMELOCRINUS Jaekel, 1902

Type species. By monotypy. *Promelocrinus anglicus* Jaekel, 1902, p. 1068, fig. 8. Ubaghs (1958, pp. 267–304) gives a detailed discussion of *Promelocrinus* and its nomenclature.

Promelocrinus anglicus Jaekel

Plates 100, 101; Plate 102, figs. 1, 2, 4.

1873 *Mariacrinus flabellatus* Salter, 1873, p. 122.
1891 *Melocrinus flabellatus* (Salter), Woods, p. 41.
1902 *Promelocrinus anglicus* Jaekel, p. 1068, fig. 8.
1926 *Melocrinus*? *spectabilis* Angelin, Springer, p. 27, pl. 5, figs. 2, 3.
1926 *Mariacrinus* sp. Springer, p. 29, pl. 5, fig. 13.
1943 *Melocrinites spectabilis* (Angelin), Bassler and Moodey, *pars*, p. 559.
1943 *Promelocrinus anglicus* Jaekel, Bassler and Moodey, p. 652.
1953 *Promelocrinus anglicus* Jaekel, Ubaghs, p. 711, fig. 82*c*.
1958 *Promelocrinus anglicus* Jaekel, Ubaghs, p. 300, text-fig. 18.
1973 *Promelocrinus anglicus* Jaekel, Webster, p. 224.
1973 *Promelocrinus anglicus* Jaekel, Brower, p. 432, text-fig. 36.

Holotype. Unnumbered specimen in the Paläontologisches Museum, Museum für Naturkunde, Berlin, DDR, 104. A poorly preserved crown on a small slab.

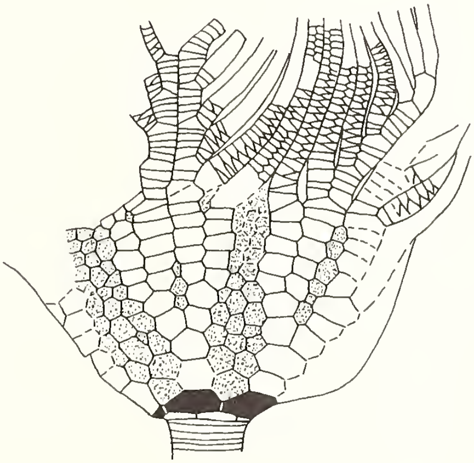
Other material. *P. anglicus* is a moderately abundant crinoid in the Dudley Limestone and I have examined approximately fifty specimens of type and nontype material. Syntypes of *Mariacrinus flabellatus* Salter: SM. (Sedgwick Museum) A10136, a crown and three stem segments; A12753–12758, partial crowns. Specimens figured by Springer (1926, pl. 5, figs. 2, 3) as *Melocrinus*? *spectabilis* Angelin: S. (Springer Collection at United States National Museum) 270. Young crown illustrated by Springer (1926, pl. 5, fig. 13) as *Mariacrinus* sp.: S. 270. Specimens figured by Ubaghs (1958, text-fig. 18) as *P. anglicus* Jaekel: SM. 12767; BMNH. (British Museum of Natural History) E26497. Specimen mentioned by Ubaghs (1958, p. 269) as

P. anglicus: BMNH. 57105. Specimens figured herein as *P. anglicus*: SM. A10136, A12767; GSM. (Geological Survey Museum) 85098, 91770, 103737; BMNH. E26498, 36848; S. 270, 271. In addition, two unidentified rooting devices are illustrated: SM. A12759, A12761. Material examined but undescribed in this paper includes SM. A36644, several specimens in A10136, A12768, A12769. GSM. 103738–103743. BMNH. 25514, 40123, 40328, 47931, 57132–57135. Several specimens in S. 270, two unnumbered specimens in the Springer Collection. UB. (University of Birmingham), Holcroft Collection 2, 260, 287, 309, 506, 511; Ketley Collection 42, 99, 112, 122. DM. (Dudley Museum) 407–412. YM. (York Museum) JCB. 74/1, 74/2.

Unidentified roots. SM. A12759–12762, A12764–12766. Salter referred a series of massive cirrus roots to this species for unknown reasons. Inasmuch as there are no known calyces of *P. anglicus* which possess this type of rooting device, no direct reason exists to assign these roots to *P. anglicus*. Possibly Salter considered the roots and crowns conspecific because they were closely associated when the specimens were originally purchased. However, this is not supported by the available material, or by any notes made by Salter, and the roots are regarded here as unidentified.

Type locality. Silurian, Wenlock. Dudley Limestone, near Dudley, West Midlands. The exact locality is unknown. The specimens were found during the last century by quarrymen, children, and other collectors. The typical locality label simply reads 'Dudley'. The Wrens Nest is the most extensively quarried of the Silurian inliers near Dudley.

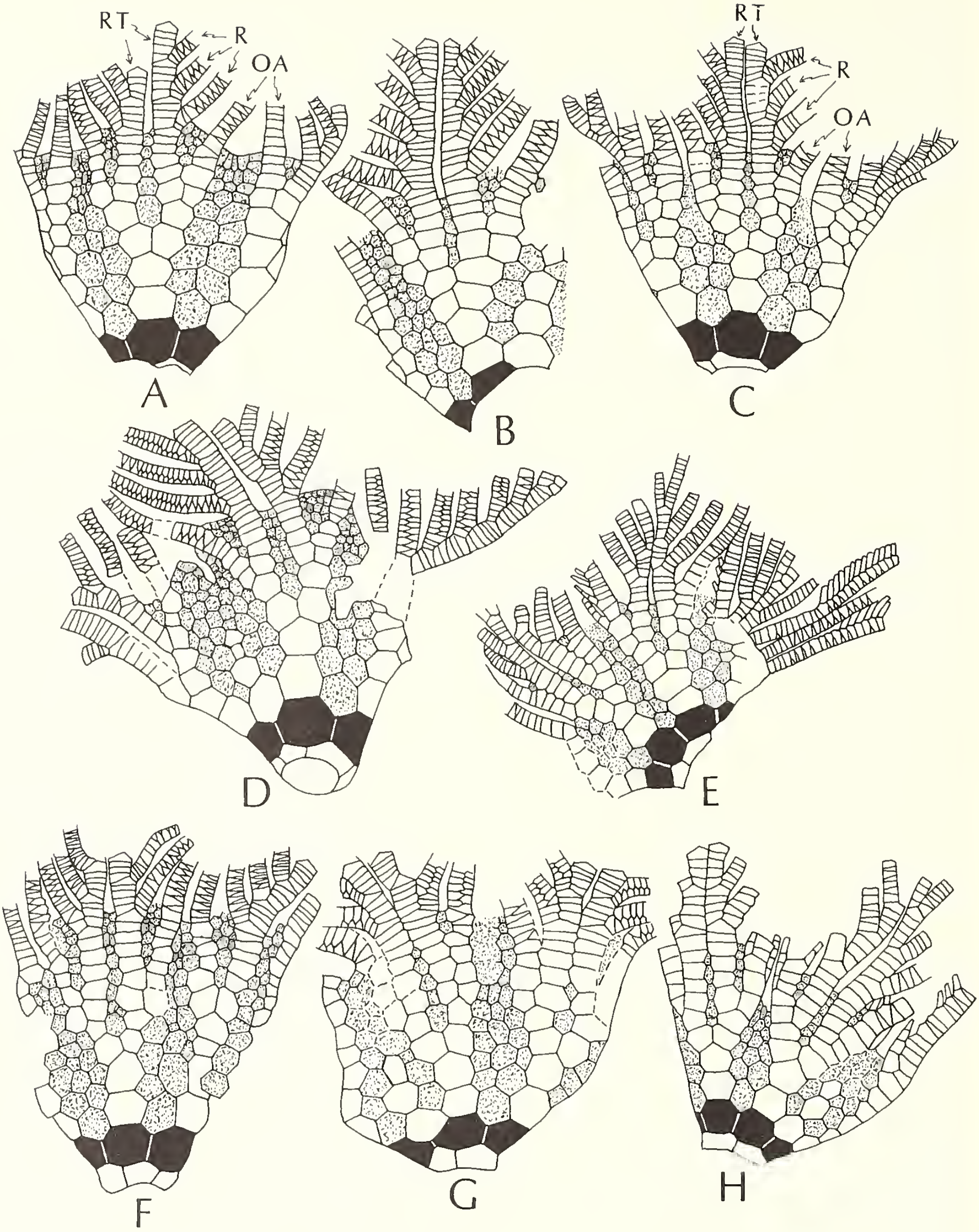
Diagnosis. A large species of *Promelocrinus* with calyx heights ranging up to about 42 mm. Numerous ramules present and the ray trunks of adults bear twelve to fifteen ramules. Adult crinoids possess biserial brachials. Calyx ornamentation variable; median-ray ridges present but these may be strongly or weakly developed; surfaces of plates sometimes smooth but usually finely granulose; aside from the median-ray ridges, the plates may be flat or somewhat swollen and nodose; a few specimens have fine multiple stellate ridges.



TEXT-FIG. 1. Holotype of *Promelocrinus anglicus* Jaekel. Lateral view of poorly preserved crown, ×2·2. Symbols: radials—black; interbrachs, intersecundibrachs, and intertertibrachs—stippled.

Description of adult. Young specimens are described in the ontogeny section. Calyx conical, generally with slightly rounded walls, height/width ratio of uncrushed specimens about 0·8. Ornamentation variable; median-ray ridges present but range from weakly to strongly developed; surfaces of plates generally covered with fine irregular granules although some smooth examples are known; aside from plates with median-ray ridges, the plates may be smooth or somewhat swollen and nodose; several examples show fine multiple stellate ridges.

Basals four, one large and three small, large basal with sutures in *B* and *E* ray positions; small basals pentagonal, height/width ratio ranges from 0·3 to 0·6; large basal six-sided, with distal margin truncated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for reception of radial, height/width ratio 0·3. Radials largest plates in calyx, hexagonal, in lateral contact in all interrays; height/width ratio varies from 0·8 to 1·0. Primibrachs slightly smaller than radials. Primibrach *1* hexagonal, height/width ratio from 0·7 to 1·0. Primibrach *2* axillary, bearing proximal secundibrachs, septagonal, height/width ratio from 0·8 to 1·0. Secundibrachs generally two per ray; rarely one or three plates are present. Secundibrach *1* hexagonal with inner sides joined; height/width ratio varies from 0·6 to 0·9. Secundibrach *2* axillary, bearing proximal tertibrachs of ray trunks and outer arms; secundibrach *2* varies from pentagonal to septagonal although six- and seven-sided plates are most common; height/width ratio ranges from 0·5 to 1·0. Lower portion of ray trunk ranging up to the proximal quartibrachs and several brachials of the first ramule are fixed into the calyx by intersecundibrachs and intertertibrachs; usually six tertibrachs are present, uniserial, lacking pinnules; shapes of nonaxillary plates ranging from four- to seven-sided, plates becoming shorter in distal direction, axillary tertibrach pentagonal or septagonal; proximal quartibrachs similar to tertibrachs except for smaller size. Six or seven tertibrachs of the outer arm fixed into calyx by interbrachs and intertertibrachs; plates like tertibrachs of ray trunks except that traces of fixed pinnules are often seen, such as on the interray side of tertibrach *2*. Interbrachial areas consist of about eleven to thirteen ranges of plates; proximal plates large and regular, becoming smaller and less regular distally; approximately five ranges of plates located below tertibrach *1* of the outer arms; interbrachial areas reach maximum width at primaxil, then become constricted above secundiaxil (see section on variation for details of plate formulae and the intersecundibrachs). Intertertibrachs small and irregular, one plate in proximal range, distal ranges consisting of one or two plates each. Primanal located between the proximal primibrachs of the *C* and *D* rays; primanal followed by three plates, the central of which is the proximal anal series plate and the two flanking ones are *CD* interray interbrachs. Anal series plates generally hexagonal; from two to five plates present, above which the anal series plates cannot be separated from interbrachs of the *CD* interray. Proximal range of *CD* interray interbrachs consists of one plate, higher ranges with one or two plates; above the level of the anal series, the *CD* interray interbrachials merge, and form ranges of three to five plates.

Full discussion of the arms is given in the sections on variation and ontogeny. Ray trunk brachials uniserial, nonpinnulate, much wider than high, nonaxillary plates roughly rectangular, axillary plates five-sided. Within a single series of plates, the proximal ones are narrowest but these expand distally so that the axillary is the widest plate in the series (text-fig. 3*j*–*l*); this ensures that the axillary gives rise to large ramule and ray trunk brachials which is required by problems of supporting the food-gathering system. Proximal brachials of ramules and outer arms uniserial but more distal brachials are pinnulate and of immature or mature biserial type. Immature biserial brachials have curved proximal and distal margins which converge on each other so that the brachials appear wedge-shaped, pinnule facets protuberant (text-fig. 3*c*–*g*). Mature biserial brachials are found in the proximal parts of ramules of several specimens; proximal and distal margins parallel to one another; inner margins sharply separated from proximal and distal ones, converging on each other; pinnule facets less protuberant than those of immature biserial brachials (text-fig. 3*h*, *k*). Well-preserved brachials show finely crenulate sutures (text-fig. 3*g*, *h*, *k*, *l*); these are not seen on weathered brachials which appear to have straight sutures. Pinnules long, slender; mature ones consist of ten or more elongate pinnulars; pinnulars with two rows of irregular covering plates (text-fig. 3*e*, *f*, *i*).

TEXT-FIG. 2. Calyces of *Promelocrinus anglicus* Jaekel. A, lateral view of SM. A12767, note relatively slender arms and complete intersecundibrachial areas, × 1·5. B, *D* ray view of S. 270, specimen identified by Springer (1926, pl. 5, fig. 3) as *Melocrinus*? *spectabilis* Angelin, the intersecundibrachial areas are complete, × 1·8. C, lateral view of GSM. 85098, a crown with interbrachial areas that are constricted at the level of the secundibrachs and proximal tertibrachs, × 1·6. D, *C* ray view of GSM. 91770, note complete intersecundibrachial areas with two plates in most ranges, × 1·6. E, lateral view of BMNH. 38648, an immature calyx, × 2·4. F, lateral view of GSM. 103737, an adult crown with complete intersecundibrachial areas, × 1·4. G, probably *C* ray view, SM. A10136, a syntype of *Mariacrinus flabellatus* Salter, note partially developed intersecundibrachial areas in which the inner arms are joined together in areas which lack intersecundibrachs, × 1·0. H, possibly *D* ray view, BMNH. E26498, a young crinoid with complete intersecundibrachial areas, × 2·6. Symbols: radials—black; interbrachials, intersecundibrachs, and intertertibrachs—stippled; in A and C, RT, R, and OA denote the ray trunks, ramules, and outer arms respectively.

Only proximal portion of column known, round, heteromorphic; column consists of five orders of plates, one order of nodals (N), and four orders of internodals (IN); proximal noditaxis complete except that 4IN are lacking; 4IN is completely developed in third or fourth noditaxis below the calyx; all plates with nodose margins except 4IN. Articular surfaces of columnals partly known; axial canal pentalobate, with lobes pointing toward the interrays as usual for monocyclic crinoids.

Variation in interbrachial areas. Promelocrinus anglicus is known from a relatively large sample consisting of about fifty specimens which allows some aspects of variation to be examined. Although there are numerous abundant species of Palaeozoic crinoids, studies of variation are surprisingly rare. Consequently, it is difficult to establish exactly how conservative are some of the basic characters that have been used in crinoid taxonomy for many years. Hopefully this study will provide some information about the interbrachial areas and arm-branching patterns of melocrinitids.

The structure of the primibrachs and the interbrachs was studied on thirty-five specimens, each of which is represented by a single data set. Most crinoids are not well enough preserved so that more than one ray and interray area can be determined. Consequently, the data only reflect variation between specimens and no information is available on variation within individuals. Owing to preservation, it is usually not possible to make complete sets of measurements on most crinoids. Most data come from the proximal parts of the rays and interbrachial areas.

The shapes of the primibrachs were seen in thirty-five specimens. Primibrach *1* is invariably hexagonal; septagonal outlines are observed on thirty-four axillary primibrachs while one plate is pentagonal. These figures show low variation and demonstrate that the shapes of these plates are largely stabilized. *Alisocrinus tetrarmatus* Brower, a primitive Ordovician melocrinitid, is characterized by greater variability (Brower 1973, p. 430).

To a large extent, all of the interbrachial areas are subject to similar variation and consequently, the interbrachs between the rays are emphasized and the other areas only briefly discussed.

The parameter measured is the number of plates in the different ranges of interbrachials. The following trends of variation are shown by the statistics in Tables 1

TABLE 1. Table showing variation of interbrachs.

Number of range (numbers increase from proximal to distal ranges of plates)	Mean number of interbrachs in listed range	Standard deviation	Percentage standard deviation [(standard deviation/mean) × 100]	Range	Number of specimens
1	1·00	0·0	0·0	—	29
2	2·00	0·0	0·0	—	29
3	2·78	0·424	15·2	2·0–3·0	27
4	2·90	0·417	14·3	2·0–4·0	24
5	3·02	0·602	19·9	2·0–4·0	21
6	3·13	0·663	21·2	2·0–4·0	19
7	3·03	0·562	18·5	2·0–4·0	16
8	2·93	0·730	24·9	2·0–4·0	14
9	2·89	0·650	22·5	2·0–4·0	9
10	3·50	1·12	31·9	3·0–5·5	5
11	3·50	1·12	31·9	3·0–5·5	5

TABLE 2. Correlation matrix for the interbrachs. (All correlation coefficients are significant at the 0·01 risk level.)

Position of interbrachial range (numbers increasing distally)	1·00	0·798	0·934	0·930
Number of interbrachs in the various ranges	0·798	1·00	0·881	0·904
Standard deviation	0·934	0·881	1·00	0·988
Percentage standard deviation	0·930	0·904	0·988	1·00

and 2. All characters are positively correlated. Proceeding from proximal to distal ranges, the average number of plates increases from 1·0 to 3·5, the standard deviations rise from nil to 1·12, and the percentage standard deviations range from nil to 32%. This theme of distally increasing number of plates and variation seems to be characteristic of most Paleozoic camerate crinoids with numerous fixed-brachs (e.g. Brower 1973, 1974). A correlation matrix was computed for the number of plates within the various ranges of interbrachs. The proximal two ranges of plates are invariant so all correlations involving these are nil. For the higher ranges, most of the significant coefficients (0·05 risk level) lie close to the diagonal of the matrix. This indicates that the number of interbrachs in a particular range is best correlated with those of the adjacent one or two ranges of plates rather than the number of plates in all ranges. The significant correlations are all positive and these vary from 0·40 to 0·96.

P. anglicus exhibits three types of intersecundibrachial areas: 1, fully developed in which the half-rays of a single ray are completely separated by intersecundibrachs (text-fig. 2*a–f*, *h*). 2, areas in which intersecundibrachs are absent and the brachials of the two half-rays are joined together; and 3, areas which are intermediate between the two above types (text-fig. 2*g*). Most intersecundibrachial areas are complete although several examples of the other two types are known. The nature of the intersecundibrachs is correlated with the amount of fusion of the inner arms. Fully developed intersecundibrachial areas comprise a primitive character in melocrinitids such as *Glyptocrinus*, *Alisocrinus*, and most specimens of *Promelocrinus*. In these forms the inner arms are not fused together. Most advanced melocrinitids, for example, *Ctenocrinus* and *Melocrinites*, exhibit intersecundibrachial areas with a reduced number of plates or the intersecundibrachs may be lacking. The inner arms of these crinoids are fused together to form a more or less solid ray trunk which provides strong support for the numerous ramules. Variation of the nature of the intersecundibrachial areas of *P. anglicus* is not surprising because the species is a large crinoid with numerous ramules which occupies an evolutionary intermediate position between *Alisocrinus* and *Ctenocrinus* (see Ubaghs 1958; Brower 1973) for evolution of melocrinitids). Tables 3 and 4 list the statistics for variation in the intersecundibrachs. As in the case of the interbrachs, all of the parameters for variation of the number of plates in the different ranges are positively correlated. From proximal to distal ranges, the average number of plates per range varies from 0·96 to 1·8, and the percentage standard deviations are also augmented from 20 to 71%. Comparison of Tables 1 and 3 shows that the percentage standard deviations for the intersecundibrachs are much larger than those of the interbrachs. Thus *P. anglicus* follows the pattern of variation seen in most Palaeozoic camerates with many fixed-brachials in that the more distal intersecundibrachs are more variable than the more proximally located interbrachs. The distribution of correlation coefficients for the different ranges of intersecundibrachs parallels that for the interbrachs except that the correlation coefficients are significant for the number of plates in almost all ranges except the most distal one. However, the number of plates in a given range is most highly correlated with the number of plates in the adjacent ranges and the degree of correlation decreases with more distant ranges. The difference in correlations between the interbrachs and the intersecundibrachs is probably because the secundibrachs are found in a more restricted and constricted area than the interbrachs. The data for the intertertibrachs are similar to those of the intersecundibrachs.

TABLE 3. Table showing variation of intersecundibrachs.

Number of range (numbers increase from proximal to distal ranges of plates)	Mean number of intersecundibrachs in listed range	Standard deviation	Percentage standard deviation [(standard deviation/mean) × 100]	Range	Number of specimens
1	0·963	0·193	20·0	0·0–1·0	27
2	1·07	0·385	35·8	0·0–2·0	27
3	1·07	0·567	52·8	0·0–2·0	27
4	1·19	0·503	42·4	0·0–2·5	27
5	1·23	0·491	39·9	0·0–2·0	25
6	1·24	0·650	52·4	0·0–2·0	24
7	1·42	0·590	39·4	0·0–2·0	21
8	1·81	1·29	71·0	0·0–6·0	17

A matrix of correlation coefficients for the number of plates of all ranges in all interbrachial areas shows that most of these correlations are not significant, which indicates that much variation between the different interbrachial areas is independent. There are two general areas of significant correlation. The number of intersecundibrachs is inversely correlated with the number of interbrachs in the fourth range. These coefficients range from −0·54 to −0·75. This is geometrically reasonable because the fourth range of interbrachs occurs at the proximal secundibrach level which is where the intersecundibrachs begin. Basically many crinoids with numerous interbrachs in the fourth range have relatively wide interbrachial areas at this level; this constricts the rays and results in a reduced number of intersecundibrachs. The reverse is observed for crinoids which show relatively small numbers of interbrachs in the fourth range in conjunction with a high number of intersecundibrachs (see text-fig. 2). Although many of the coefficients are not significant, the number of intertertibrachs is generally positively correlated with the number of intersecundibrachs (correlation coefficients range from nil to 0·74).

Summarizing, for a given interbrachial area the number of plates in each range and the variation of number of plates increases distally. The intersecundibrachial and intertertibrachial areas are more variable than the interbrachial areas. The number of plates in a given range is most highly correlated with the number of plates in the

TABLE 4. Correlation matrix for the intersecundibrachs. (All correlation coefficients are significant at the 0·05 risk level; those in italics are also significant at the 0·01 level.)

Position of intersecundibrachial range (numbers increasing distally)	1·00	*0·917*	0·819	0·725
Number of intersecundibrachs in the various ranges	*0·917*	1·00	*0·908*	0·730
Standard deviation for number of plates in the various ranges	0·819	*0·908*	1·00	*0·930*
Percentage standard deviation	0·725	0·730	*0·930*	1·00

adjacent ranges and less well correlated with plates that are further away. The number of plates in the interbrachial, intersecundibrachial, and intertertibrachial areas shows much independent variation. However, the number of intersecundibrachs is somewhat positively correlated with the number of intertertibrachs and the number of intersecundibrachs is inversely related to the number of interbrachs at the secundibrach level.

Variation in arm-branching pattern. The number of brachials was counted at various strategic points, including the number of secundibrachs, tertibrachs, and the brachials separating the various ramules. Up to 162 rays could be seen in fifty-one specimens. It is not possible to compile complete sets of data for several reasons. Almost all crinoids are preserved on slabs and some of the rays cannot be determined because they are buried in matrix. Anywhere from one to ten half-rays could be measured on individual specimens. Most visible rays are not complete and the distal tips of the arms are missing. In smaller specimens the arms have not fully developed (see later discussion of ontogeny), and the higher brachials and ramules had not formed when these individuals died. Thus most information is derived from the proximal part of the arms.

In the first step of the analysis, variation within the arms of single specimens was investigated relative to variation between specimens. F-ratios indicate that there is no significant difference in variation patterns within and between the specimens. Consequently, all subsequent discussion will only treat variation between specimens. Each data point comprises the average number of secundibrachs, etc., for a single crinoid. The following general trends are noted in the statistics of Table 5. The percentage standard deviations (i.e. (standard deviation/mean) × 100) range from 8·9 to 16·7%. These values are roughly similar to those of many camerate crinoids (e.g. systematic descriptions of Brower 1973). The mean number of secundibrachs is 2·08. Almost all crinoids have two secundibrachs; most variant half-rays are characterized by three plates. If three plates are present, these are shorter than those of the normal half-rays with two plates. The average number of tertibrachs comprises 5·99 plates and the number varies from five to seven plates. Within a single crinoid, the total number of secundibrachs and tertibrachs is generally constant or almost so. In a half-ray with an extra secundibrach, the tertibrachial series usually possesses one less plate than the normal neighbouring half-rays. The result of this pattern is that the proximal ramule of the adjacent half-rays occurs at the same level. This is necessary to ensure that each half-ray develops equally and filters the same amount of water.

TABLE 5. Table showing variation of arm-branching pattern.

Parameter	Mean	Standard deviation	Percentage standard deviation [(standard deviation/ mean) × 100]	Range	Number of specimens
Number of secundibrachials	2·09	0·297	14·2	1·0–2·5	51
Number of tertibrachials	5·99	0·532	8·89	5·0–7·0	50
Number of brachials between listed ramules					
1 and 2	4·23	0·500	11·8	3·0–5·0	51
2 and 3	4·62	0·632	13·7	3·0–6·0	49
3 and 4	5·02	0·674	13·4	4·0–7·0	45
4 and 5	5·22	0·668	12·8	4·0–6·5	37
5 and 6	5·18	0·611	11·8	4·0–6·0	31
6 and 7	5·20	0·705	13·6	4·0–7·0	27
7 and 8	5·13	0·830	16·2	3·5–6·0	20
8 and 9	4·93	0·720	14·6	3·5–6·0	16
9 and 10	5·39	0·858	15·9	4·0–7·0	9
10 and 11	6·06	0·943	15·6	5·0–8·0	8
11 and 12	5·4	0·548	10·1	5·0–6·0	5
12 and 13	5·8	0·837	14·4	5·0–7·0	5
13 and 14	6·0	1·000	16·7	5·0–7·0	3

Turning to parts of the arms which bear the ramules, the average number of brachials separating the adjacent ramules ranges from 4·23 to 6·06 as listed in Table 5. The relationships between ramule position, number of plates between the adjacent ramules, the standard deviations, and the percentage standard deviations are given by the correlation matrix in Table 6. Inspection of the correlation matrix shows that the number of plates separating the ramules, the standard deviations, and the position of the ramules are all positively correlated at the 0·01 risk level. The average number of plates and the variation of number of plates increases proceeding from proximal to distal parts of the arms. This general pattern is common in many Palaeozoic crinoids (e.g. systematic descriptions in Brower 1973). The percentage standard deviations which show relative dispersion are not significantly correlated with position of the ramules or average number of plates although the correlation between standard deviation and percentage standard deviation is significant.

A correlation matrix was also calculated for numbers of plates between the ramules. Several of these correlations are significant at the 0·05 and 0·01 levels, namely those involving plates in the middle of the arms ranging from above the fourth ramule to below the eighth ramule. These correlations range from 0·49 to 0·67. Within this

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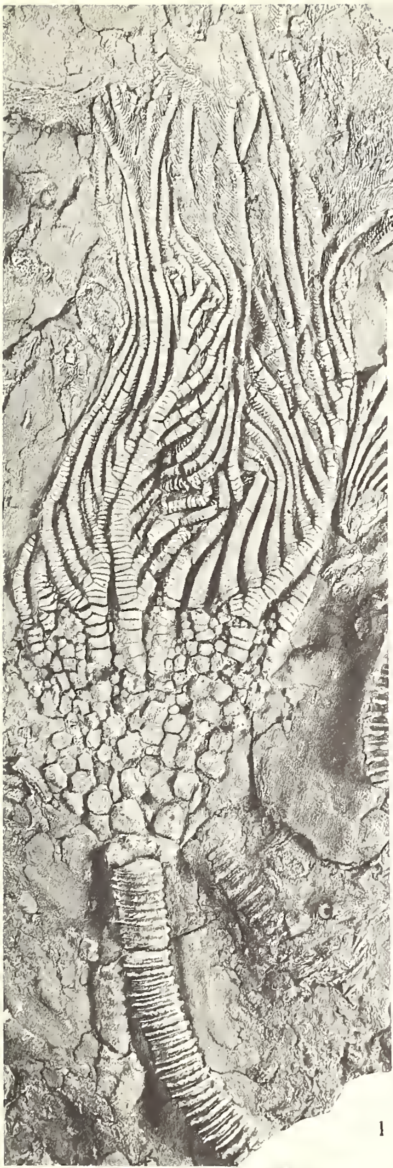
EXPLANATION OF PLATE 100

Promelocrinus anglicus Jaekel. 1, lateral view of GSM. 103737, a complete adult crown with thirteen ramules, ornamentation consists of nodose plates covered with granules, intersecundibrachial areas complete, × 1·25. 2, possibly *D* ray view, BMNH. E26498, a young crown with four ramules, plates with median-ray ridges and fine granules, × 2. 3, *D* ray view of S. 270, a small adult with complete intersecundibrachial areas, plates covered with median-ray and fine multiple stellate ridges, × 1·5. 4, lateral view of BMNH. 38648, a young specimen with four ramules, ornamentation includes median-ray ridges and finely granulose plates, × 1·75.



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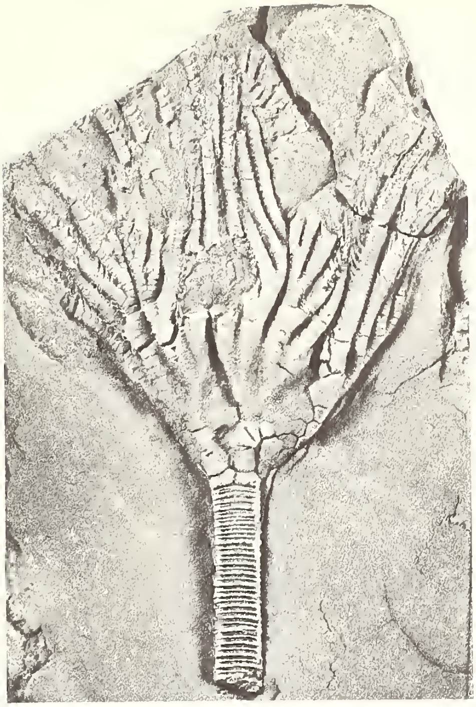

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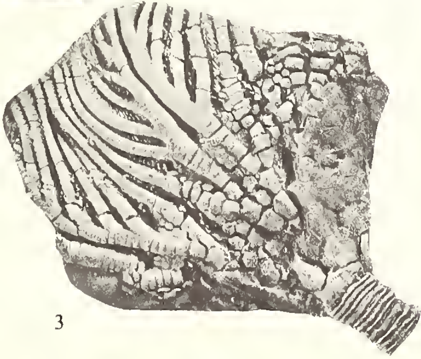

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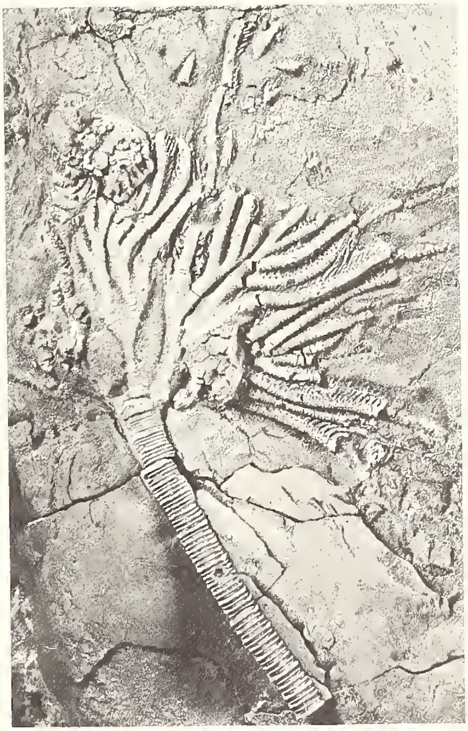

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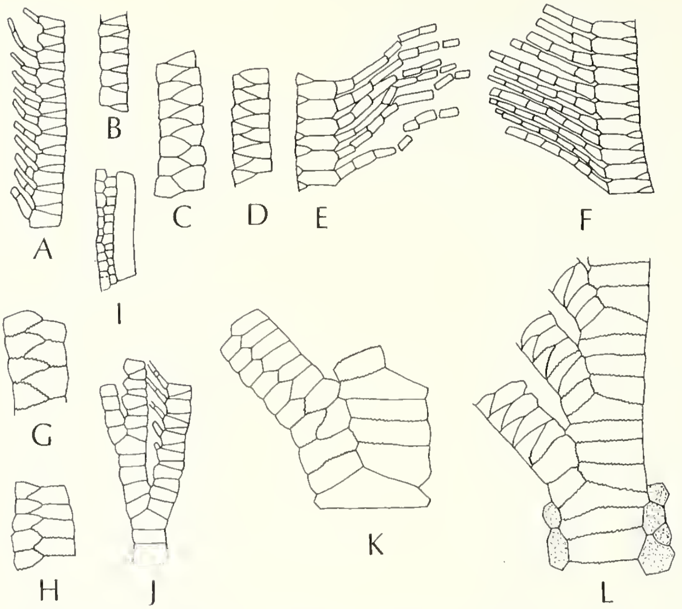
BROWER, Wenlock crinoids



TEXT-FIG. 3. *Promelocrinus anglicus* Jaekel. A–H, ramule and outer arm fragments, ×7·0; A, side view of uniserial brachials, BMNH. E26498; B, side view of immature biserial brachials, BMNH. 38648; C and D, front views of immature biserial brachials, S. 270 and GSM. 85098 respectively; E and F, side views of immature biserial brachials with complete or nearly complete pinnules, S. 271 and GSM. 85098 respectively; G and H, front views of immature biserial brachials showing crenulate sutures, GSM. 85098 and 91770 respectively. I, ventral view of pinnular with covering plates, GSM. 85098, ×28·0. J–L, fragments of ray trunks and associated ramules; J, second and third ramules of BMNH. E26498, an immature specimen, note uniserial brachials of ramule and small number of ramule brachials which are joined to the adjacent ray trunks, ×7·0; K, first ramule of SM. A10136, a large adult in which numerous ramule brachials are joined to the adjacent part of the ray trunks, the ramule has mature biserial brachials, crenulate sutures are well developed, ×7·0; L, first through third ramules of SM. A12767, an adult crown, ray trunk fragment similar to the previous figure except for immature biserial brachials in the ramules, ×5·5. Interbrachials are stippled in L.

interval, a given number of brachials is positively correlated with the number of plates separating the adjacent pairs of ramules. Apart from this, the correlation coefficients are not significant, indicating that these parameters largely vary independently of one another. This is despite the fact that the number of brachials separating the ramules tends to increase distally.

Once the ramules have formed, the number of plates between the adjacent ramules is fixed. All new brachials form at the distal tips of the arms or ramules and no new plates are intercalated between those previously present. There is no significant

TABLE 6. Correlation matrix indicating relationships between the various ramule spacing parameters. (Correlation coefficients which are significant at the 0·01 and 0·05 risk levels are in italics.)

Position of ramules (numbers increasing distally)	1·00	*0·861*	*0·688*	0·411
Number of plates separating adjacent ramules	*0·861*	1·00	*0·790*	0·459
Standard deviation	*0·688*	*0·790*	1·00	*0·905*
Percentage standard deviation	0·411	0·459	*0·905*	1·00

correlation between these counts of brachials and the age or size of the crinoid. In other words, these characters are constant regardless of size of the animal. Consequently it is concluded that these were not subject to natural selection which operated over the observed ontogeny of the species.

Nomenclature. As indicated by Ubaghs (1958, p. 267) the nomenclature has been confusing in the past, notably by *Mariacrinus flabellatus* Salter, 1873 which is a *nomen nudum* (and later put into *Melocrinus* by Woods 1891).

Comparison. Promelocrinus anglicus differs from *P. fulminatus* (Angelin) (see Ubaghs 1958) and *P. radiatus* (Angelin, 1878) (see Ubaghs 1958) from the Wenlock of Sweden as follows: 1, the Swedish specimens are much smaller (calyx height ranges from 6 mm to about 18 mm), whereas adult specimens of *P. anglicus* exhibit calyx heights up to approximately 42 mm. 2, *P. fulminatus* and *P. radiatus* bear one or two ramules in each half-ray whereas equivalent-sized individuals of *P. anglicus* possess four, five, or more ramules. Adults of *P. anglicus* are characterized by twelve to fifteen ramules. 3, the Swedish crinoids have stellate ridges on the interbrachs which are lacking on typical examples of *P. anglicus*. 4, in *P. fulminatus*, nodes occur on the side of the brachials with the pinnule facets but the brachials of *P. anglicus* are comparatively smooth. 5, the brachials in the ramules and outer arms of *P. radiatus* are uniserial but immature biserial brachials are found in equivalent-sized specimens of *P. anglicus* (calyx height roughly 18 mm). However, both *P. fulminatus* and young specimens of *P. anglicus* (calyx height approximately 7 mm) show uniserial brachials.

P. anglicus has been confused with *Ctenocrinus spectabilis* (Angelin, 1878) (see Ubaghs 1958) from the Silurian of Sweden by Springer (1926) and Bassler and Moodey (1943, p. 559). The ctenocrinid differs in several features. The proximal parts of the ray trunks of the ctenocrinid are fused whereas those of *P. anglicus* are separate. In *C. spectabilis* the ramules of the ray trunk are usually separated by six or seven plates in contrast to the four to six plates of *P. anglicus*. The lectotype of *C. spectabilis* is characterized by a calyx height of around 15 mm and uniserial brachials. Immature biserial brachials are present in juvenile crowns of *P. anglicus* which are about the same size.

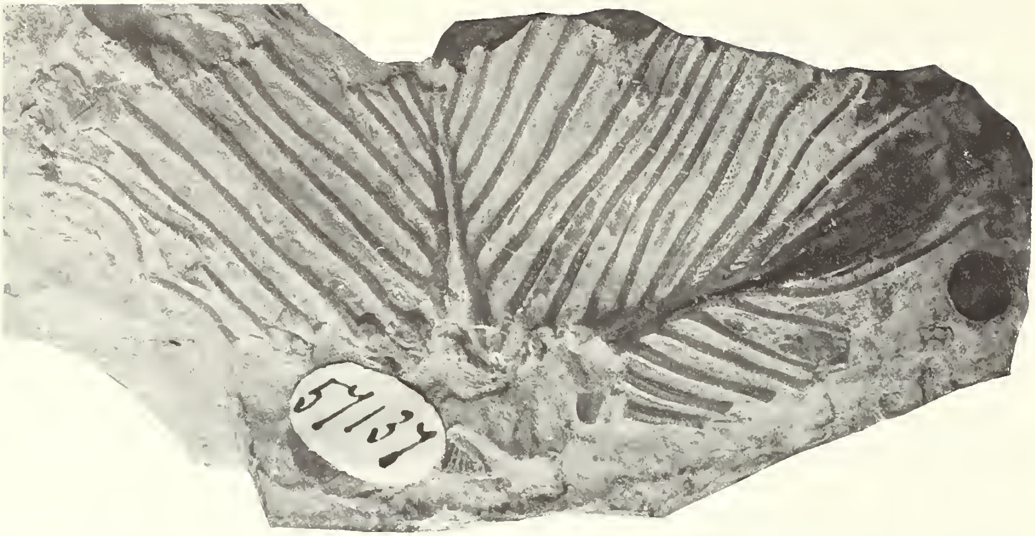
Promelocrinus sp.

Text-fig. 4

1958 *Promelocrinus* sp., Ubaghs, p. 299, text-fig. 17*a*.
1973 *Promelocrinus* sp., Webster, p. 225.

Locality. Silurian, Wenlock. Dudley Limestone, near Dudley, West Midlands, probably Wrens Nest Inlier.

Remarks. This form is represented only by a single specimen in matrix showing parts of two rays (BMNH. 57137). Unlike most specimens, the arms are preserved in the outstretched or food-gathering position. The nature of the ray trunks indicates assignment to *Promelocrinus* with no doubt. The presence of at least seven ramules in conjunction with ray trunk arms or inner arms that are not fused together is diagnostic even though the dorsal cup is unknown. Other melocrinitids, such as *Ctenocrinus*,



TEXT-FIG. 4. *Promelocrinus* sp. Dorsal view of BMNH. 57137, the arms are preserved in food-gathering orientation, × 1·9.

with well-developed ray trunks are characterized by inner arms which are wholly or partially fused together (for example, see Ubaghs 1958, pp. 279, 293–304). *Lampterocrinus*, a dicyclic crinoid with ray trunks, has only one ray trunk arm per ray in contrast to the two ray trunk arms in each ray of *Promelocrinus* (see Springer 1926). *Promelocrinus* sp. is not conspecific with either *P. anglicus* or *P. fulminatus* (Angelin) (see Ubaghs 1958) from the Wenlock of Gotland, which has one ramule whereas the English form has at least seven ramules. In addition, *P. fulminatus* has nodose brachials on the ray trunk which are more massive and wider relative to height than the non-nodose brachials of this crinoid. In *P. anglicus*, crinoids bearing ray trunks of this size are characterized by ramules and outer arms with biserial brachials in contrast to the uniserial brachials of *Promelocrinus* sp. This crinoid is most closely related to *P. radiatus* (Angelin) (see Ubaghs 1958) which is also found in the Wenlock of Gotland. Unfortunately, *P. radiatus* cannot be completely characterized because the arms are not fully known except in one immature specimen. *Promelocrinus* sp. and

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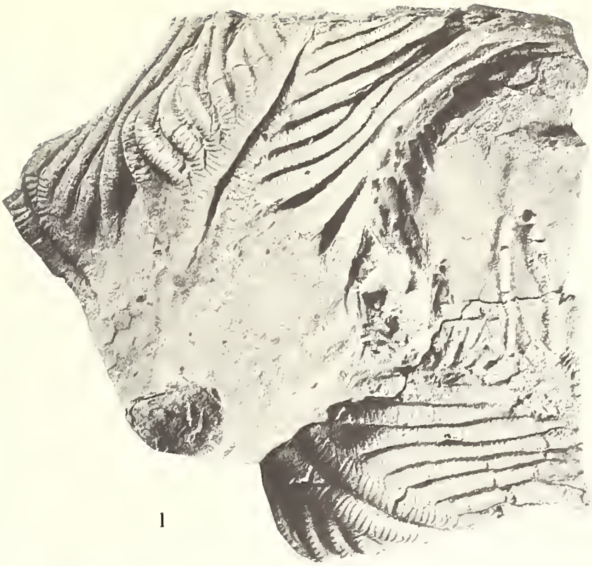
EXPLANATION OF PLATE 101

Adult specimens of *Promelocrinus anglicus* Jaekel. 1, *D* ray view of S. 270, crown figured by Springer (1926, pl. 5, fig. 3) as *Melocrinus*? *spectabilis* Angelin, note broken base which was restored in Springer's figure, the specimen is weathered so that the calyx plates seem smooth. 2, *C* ray view of SM. A10136, syntype of *Mariacrinus flabellatus* Salter, a weathered specimen with median-ray ridges and finely granulose calyx plates, intersecundibrachial areas are incompletely developed. 3, lateral view of GSM. 85098, a partial crown with ornamentation like that of fig. 2, intersecundibrachial areas are complete. 4, *C* ray view of GSM. 91770, a crown which was buried with the arms partially spread, note slightly swollen calyx plates with granulose surfaces and complete intersecundibrachial areas. All figures × 1·5.



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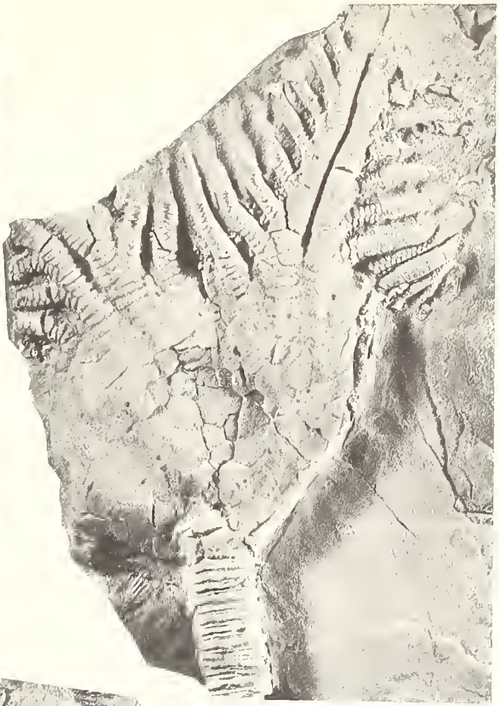

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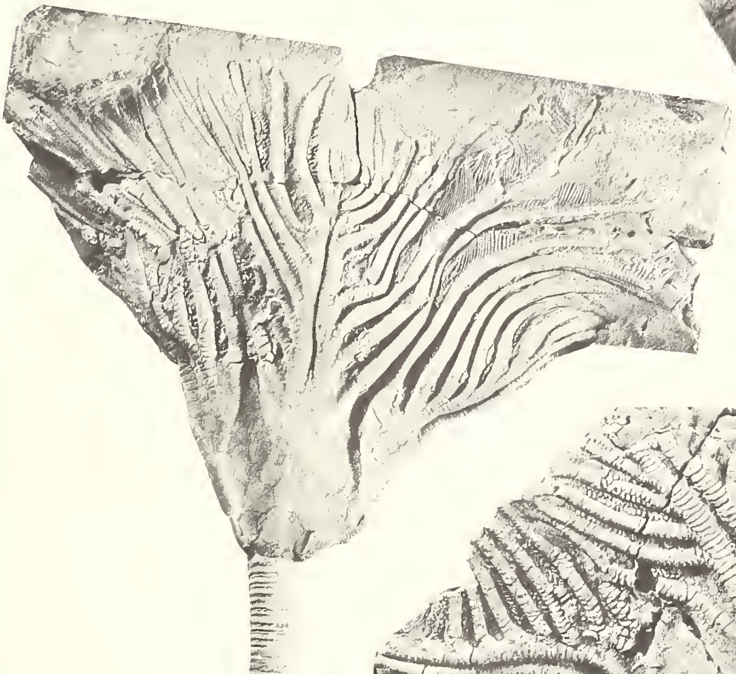

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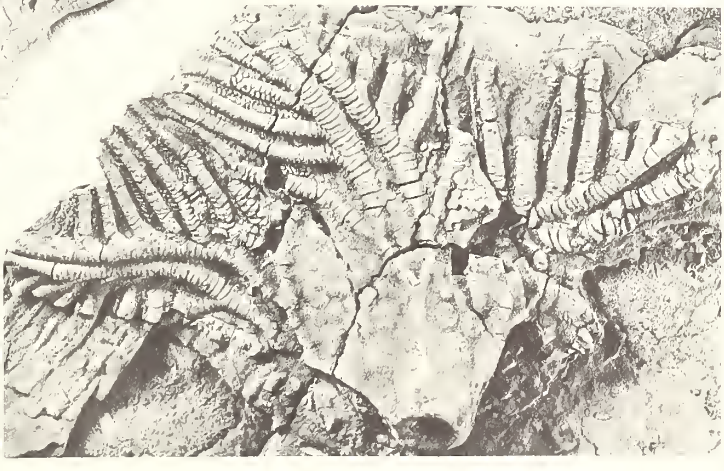

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BROWER, Wenlock crinoids

P. radiatus resemble each other in having relatively high uniserial brachials throughout the arms and the two crinoids might belong to the same species. However, this cannot be definitely determined until adult specimens of *P. radiatus* with reasonably complete ray trunks have been found.

ONTOGENY OF *PROMELOCRINUS ANGLICUS*

Ontogeny and phylogeny are intimately related in melocrinitids because the group evolved through 'mutations' (used in most general sense, to include gene changes, chromosome additions, deletions, etc.) which affected the ontogeny of young crinoids by causing divergences that were accentuated throughout subsequent development (Ubaghs 1958, pp. 293-304; Brower 1973, pp. 328-331, 432-437). Reasonably complete ontogenetic sequences are available for several species in the lineage, namely *Glyptocrinus decadactylus* Hall of the Upper Ordovician (see Wachsmuth and Springer 1897 for drawings of adults; young specimens have never been illustrated) and *Alisocrinus tetrarmatus* Brower of the Upper Ordovician (Brower 1973), both of which are primitive forms lacking ray trunks; *P. anglicus* of the Wenlock, a moderately advanced form; and *Ctenocrinus paucidactylus* (Hall) of the Lower Devonian (Goldring 1923; Brower 1974), an advanced ctenocrinid. The most interesting aspect of *P. anglicus* is the development of the food-gathering system and its comparative ontogeny with that of other crinoids. The following measurements have been made on the thirteen crinoids in the growth sequence. 1, 'size' which is height from the base of the calyx to the distal margin of the primaxil. This is the standard measure of relative age in camerate crinoids. Larger crinoids are considered chronologically older than smaller ones. 2, calyx height. Measured from the base of the calyx to the distal intersecundibrach. 3, distal fixed-brachial in the intersecundibrachial areas. For statistical purposes, this character is coded in a numerical scale in which the proximal and distal margins of tertibrach *2* are assigned values of 14 and 15, respectively, and so on. 4, calyx width. Measured from the centre of two adjacent rays at the level of the primaxil. 5, number of ramules in a half-ray. 6, length of and number of plates in the ray trunk (the initial part of the ray trunk begins at the proximal tertibrach). 7, length of and number of brachials in the free parts of the outer arms. 8, length of and number of brachials in the average ramule. All complete ramules on one individual are measured and the average determined. 9, length of and number of pinnulars in the average pinnule. A reasonable number of complete pinnules is used to estimate the average. 10, length of and number of plates in the entire food-gathering system (see later discussion for formulae).

The basic statistics derive from the simple power function or allometric equation $Y = b . X^k$ (Huxley 1932 and Gould 1966, for derivation and discussion of the equation), in which X and Y are the independent and dependent variables, respectively. A reduced major axis procedure (Imbrie 1956; Hayami and Matsukuma 1970) was selected for fitting the equations rather than the least squares method (Sokal and Rohlf 1969). This technique has the advantage of yielding slopes which are not biased by the choice of independent and dependent variables.

Growth of the calyx. As in most crinoids with many fixed-brachs, new brachials were incorporated into the calyx throughout ontogeny although the rate of fixation is most rapid in the youngest animals and declines with increasing 'size' and age (equation 1, Table 7). The smallest crinoids ('size' 5·5 mm) have tertibrach *3* joined into the calyx (text-fig. 2*e*, *h*). When a 'size' of 12–14 mm was attained, the highest fixed-brach ranges from tertibrach *6* to *10* (text-fig. 2*a*, *b*, *d*, *f*, *g*). Tertibrach *10* forms the highest fixed-brach in the largest crinoid, 'size' 20·5 mm. The nature of brachial fixation is similar to that of most camerate crinoids (see Brower 1973, p. 310; 1974, p. 14). Before incorporation into the calyx, the brachials and pinnulars resemble the higher free brachials and pinnulars. During and soon after fixation into the calyx, these plates develop angular margins along which the interbrachs, intersecundibrachs, etc., join them into the cup. The formation of these angular margins involves complex changes in the various width growth rates of the brachials and pinnulars. The fixed-brachs are differentiated from the interbrachs throughout ontogeny by larger size and the presence of median-ray ridges. To a lesser extent, the same is true of fixed-pinnulars during the early stages of incorporation; however, these differentiating features gradually disappear throughout subsequent ontogeny and eventually the pinnulars cannot be separated from the surrounding interbrachs. The origin of the fixing interbrachs is uncertain but these probably represent interambulacrals of the tegmen which become incorporated into the calyx (Brower 1973, 1974).

The calyx height is augmented throughout ontogeny during which the calyx height grows slightly more rapidly than one would predict based on ideal geometry (equation 2, Table 7). Two processes are involved in the development of calyx height, namely the incorporation of new plates into the calyx and the height growth rates of old plates. The ontogeny of calyx width relative to 'size' is isometric (equation 3, Table 7). All growth of calyx width represents calcite accretion on to previously present plates and new plates were not intercalated between old ones during ontogeny.

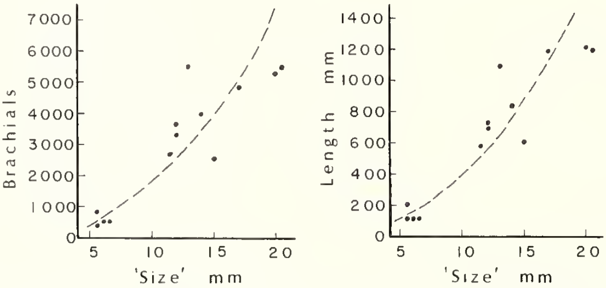
TABLE 7. Table giving equations for growth of calyx and components of the food-gathering system relative to 'size' in *Promelocrinus anglicus*. Independent variable for all equations is 'size'. 'Sizes' of smallest and largest crinoids are 5·5 and 20·5 mm. The ideal exponent equals 1·0 for all equations.

Equation number	Dependent variable (y)	Initial intercept	Exponent	Predicted minimum Y	Predicted maximum Y	Correlation coefficient	Standard error for slope
1	Distal fixed-brach in intersecundibrachial areas	7·62	0·447	16·3	29·4	0·981	0·0241
2	Calyx height mm	1·66	1·07	10·3	42·1	0·970	0·0716
3	Calyx width mm	1·36	0·998	7·44	27·6	0·955	0·0820
4	Brachials in outer arm	13·6	1·25	115·0	596·0	0·930	0·127
5	Length of outer arm mm	3·12	1·22	25·2	126·0	0·942	0·114
6	Brachials in ray trunk	2·67	1·18	20·0	94·8	0·925	0·124
7	Length of ray trunk mm	0·983	1·39	10·6	65·9	0·950	0·121
8	Number of ramules	0·614	1·11	4·07	17·5	0·938	0·107
9	Number of brachials in average ramule	11·3	1·19	86·4	414·0	0·911	0·137
10	Length of average ramule mm	2·63	1·16	19·0	87·2	0·926	0·121

Ontogeny of components of the food-gathering system. The earliest growth stages of the food-gathering system are unknown and the youngest crinoids, 'size' 5·5 mm, possess juvenile ray trunks with four ramules and half-rays containing 200–500 brachials (text-fig. 2*e*, *f*; Pl. 100, figs. 2, 4). The largest crinoids exhibit 'sizes' of around 20·5 mm and complex food-gathering systems in which the ray trunks bear up to fifteen ramules and about 5500 brachials in a half-ray (see Pl. 100, fig. 1; Pl. 102, fig. 2 for nearly complete crowns of large adults). The equation data for development of the components of the food-gathering system (Y or dependent variable) relative to 'size' (X or independent variable) are listed in Table 7. In all cases, the ideal exponent equals 1·0 because both variables are linear dimensions. Note that the observed exponents all exceed the ideal value, although in some instances the differences are not statistically significant. This indicates that the components of the food-gathering system grow more rapidly with respect to size of the calyx than one would predict based on ideal geometrical considerations. In other words, growth of these parameters is subject to positive allometry.

The outer arms remain unbranched and these constitute a subordinate part of the food-gathering system throughout ontogeny while the inner arms gradually become hypertrophied into highly ramified ray trunks which dominate the entire food-gathering system. The growth of the outer arms follows the pattern established in ancestral glyptocrinids with four arms in each ray such as *Alisocrinus tetrarmatus* (see Brower 1973). New brachials form at the distal tips of the arms (equation 4, Table 7). Young crinoids have outer arms with roughly 130 brachials while adults are characterized by about 460 plates. Largely due to the addition of new plates, the length of the outer arms rises from about 30 mm to a maximum of 113 mm (equation 5, Table 7). Growth of the outer arms is similar to the ramules as discussed later.

New brachials are added to the ray trunk throughout life (equation 6, Table 7). All embryonic plates form at the distal tips of the ray trunks and new plates are not intercalated between those previously present. All plates in a ray trunk are uniserial, either being axillary to ramules and higher brachials of the ray trunk or uniserial and nonpinnulate. The smallest crinoids show about twenty brachials in the ray trunk whereas roughly seventy-five brachials are present in the largest specimens. The length of the ray trunks rises throughout ontogeny due to the addition of new plates



TEXT-FIG. 5. Graphs showing the ontogeny of the length and number of brachials in a half-ray relative to 'size' for *Promelocrinus anglicus* Jaekel.

as just mentioned and increasing height of the previously formed plates (equation 7, Table 7). The ray trunks of the youngest and oldest crinoids are about 11 mm and 55 mm long respectively. The distal tips of the ray trunks are only known in several specimens in which these consist of four or five small brachials that are uniserial and nonpinnulate (see Ubaghs 1958, text-fig. 17*c*–*e*).

New ramules form throughout the observed ontogeny and four or five ramules occur in the youngest crinoids but mature adults ('size' 17·0–20·5 mm) may have anywhere from twelve to fifteen ramules (equation 8, Table 7). Although some variation in number of ramules exists in mature crinoids, there is no indication that various individuals attain a certain number of ramules after which new ones cease to develop. As far as can be determined, the crinoids continue to initiate new ramules throughout ontogeny. Both the number of brachials in and the length of the average ramule continue to increase during the observed ontogeny (equations 9, 10, Table 7). All new plates first appear at the distal tip of the ramule. The ramules of young crinoids are characterized by 70–130 brachials and lengths varying from 17 to 30 mm. The same figures for adults comprise about 350 brachials and 75 mm. As in the ray trunks, two processes interact to increase the length of a ramule, namely the rate of supply of new plates at the distal tips of the ramules and the rate of height growth of old plates. The dominant factor is the plate supply rate. This is shown by the fact that the height of the average brachials in the ramules ranges from 0·19 to 0·25 mm regardless of age. However, some increase in ramule length represents changes in height of the component plates because brachials of the same ramule do become higher throughout ontogeny. For example, the proximal brachials of the first ramule have heights of about 0·5 mm in the smallest crinoids and 0·7 mm in the largest. These data demonstrate that most height increase of brachials takes place early during ontogeny of the plates as in other camerates studied by Brower (1973).

During ontogeny the brachials of the ramules and outer arms undergo systematic changes. All brachials are pinnulate except for a few of the proximal plates. Some of the smallest specimens exhibit uniserial brachials; most larger crinoids have immature biserial brachials and a few of the largest specimens possess mature biserial brachials in the proximal parts of the ramules. Several features can be related to problems of supporting the growing arms and ramules. In small specimens, only one or two of the proximal brachials in a ramule are joined to the adjacent plates of the ray trunks. As the ramules become longer and heavier, several more of the proximal brachials in the ramule are fused to the ray trunk to better support the ramules. The ray-trunk brachials of young crinoids are comparatively slender and graceful but those of mature crinoids are much wider and heavier—apparently in response to a need for better support (compare crinoids in text-fig. 3). Unlike more advanced melocrinitids such as *Ctenocrinus paucidactylus* (Hall), the inner arms of *Promelocrinus anglicus* do not fuse together to provide better support for the arms.

Table 8 lists data for the development of the number of brachials and length of the arms in a half-ray for *P. anglicus* and various other species. If the reader wishes to visualize the total number of brachials and the entire length of the arms, then the half-ray figures and the initial intercepts of the equations should be multiplied by 10·0 because each crinoid has ten half-rays. All variables, 'size', length of half-ray, and brachials in a half-ray are linear dimensions so the ideal exponent is 1·0. The

TABLE 8. Table giving equations for development of the arms in a half-ray relative to 'size' for *Promelocrinus anglicus* and other crinoids. Independent variable for all equations is 'size'. Equations 1–4 were fitted by the reduced major axis method whereas 5–16 were computed by least squares. However, the correlation coefficients are high enough so the equations fitted by both techniques can be compared with little loss of information.

Equation number	Species	Dependent variable (y)	Initial intercept	Exponent	Minimum 'size' (x) mm	Predicted minimum y	Maximum 'size' (x) mm	Predicted maximum y	Correlation coefficient	Standard error for slope
1	*Promelocrinus anglicus*	Brachials per half-ray	14·1	2·09	5·5	496·0	20·5	7730·0	0·934	0·207
2	*Promelocrinus anglicus*	Length of half-ray mm	3·78	2·02	5·5	117·0	20·5	1660·0	0·946	0·182
3	All melocrinitids	Brachials per half-ray	2·12	2·22	4·0	46·3	28·0	3500·0	0·631	0·310
4	All melocrinitids	Length of half-ray mm	2·03	1·91	4·0	28·5	28·0	1180·0	0·730	0·234
5	*Alisocrinus tetrarmatus*	Brachials per half-ray	9·38	1·49	1·1	10·80	6·7	160·0	0·978	0·0994
6	*Alisocrinus tetrarmatus*	Length of half-ray mm	2·12	1·73	1·1	2·50	6·7	57·6	0·970	0·138
7	*Eopatelliocrinus scyphogracilis*	Brachials per half-ray	7·38	1·10	1·15	8·60	7·7	70·0	0·893	0·148
8	*Eopatelliocrinus scyphogracilis*	Length of half-ray mm	1·91	1·35	1·15	2·31	7·7	30·0	0·945	0·124
9	*Eopatelliocrinus latibrachiatus*	Brachials per half-ray	8·21	1·29	1·15	9·82	5·0	65·1	0·916	0·199
10	*Eopatelliocrinus latibrachiatus*	Length of half-ray mm	1·76	1·52	1·15	2·17	5·0	20·4	0·935	0·205
11	*Macrostylocrinus pristinus*	Brachials per half-ray	6·60	1·47	1·0	6·60	7·0	116·0	0·952	0·136
12	*Macrostylocrinus pristinus*	Length of half-ray mm	1·47	1·47	1·0	1·47	7·0	36·2	0·964	0·161
13	*Ptychocrinus splendens*	Brachials per half-ray	6·32	1·53	2·1	19·7	12·7	312·0	0·931	0·161
14	*Ptychocrinus splendens*	Length of half-ray mm	1·52	1·74	2·1	5·50	12·7	126·0	0·948	0·156
15	*Ptychocrinus fimbriatus*	Brachials per half-ray	9·69	0·784	2·3	18·6	7·5	47·0	0·960	0·114
16	*Ptychocrinus fimbriatus*	Length of half-ray mm	3·48	0·674	2·3	6·11	7·5	13·6	0·977	0·073

earliest specimens of *P. anglicus* probably have four equal-sized arms in a ray in which pinnules are present in the two outer arms but lacking in the two inner arms. During later ontogeny the outer arms remain unbranched although new brachials form and the length of the arms increases. The inner arms gradually become hypertrophied into highly ramified ray trunks. The length of the ray trunk is augmented throughout ontogeny by growth of new brachials and height increase of old plates. As new brachials are added to the ray trunk, new ramules are initiated. Once the ramules appear, new brachials appear at the distal tips of the growing ramules. Young crinoids have half-rays which are 100–200 mm long with about 400–800 brachials. In mature crinoids, up to 5500 brachials may be present in half-rays in which the arms are up to 1200 mm long (text-fig. 5). The equations for development of the arms in *P. anglicus* are (equations 1, 2, Table 8).

$$(\text{Length of arms}) = 3{\cdot}78\ (\text{`size'})^{2{\cdot}02}$$
$$(\text{Number of brachials}) = 14{\cdot}1\ (\text{`size'})^{2{\cdot}09}$$

In both cases the ideal exponent is 1·0 whereas the observed exponents are 2·02 and 2·09. The implication is that the development of the type of ray trunks seen in *P. anglicus* and other melocrinitids roughly squares the rate of increase of number of brachials and length of the arms relative to idealized crinoids. The *P. anglicus* figures are similar to the equations calculated in a preliminary study of evolution of melocrinitids and allied forms. The data are derived from adult crinoids of thirty-one species ranging from middle Ordovician to upper Devonian in age (equations 3, 4, Table 8). General discussions of the evolution of melocrinitids are available in Ubaghs (1958) and Brower (1973). The most primitive crinoid in the sequence, *Glyptocrinus ornatus* Billings of the middle Ordovician (Wachsmuth and Springer 1897), has only two unbranched arms in each ray. The next step in evolution of melocrinitids is the acquisition of four arms in each ray as seen in the upper Ordovician *Alisocrinus tetrarmatus* Brower. Throughout later evolution, the inner arms gradually became hypertrophied into extensively ramified ray trunks which completely filtered the water surrounding the crinoid. The primitive species of *Promelocrinus* from the Silurian of Gotland, *P. fulminatus* (Angelin) (see Ubaghs 1958) and *P. radiatus* (Angelin) (see Ubaghs 1958), have only a few ramules but some advanced species of *Melocrinites* exhibit up to thirty or thirty-five ramules in a half-ray, for example, the Devonian species *M. acicularis* Follmann (Schmidt 1941), *M. malcontractus* (Schmidt 1934), and *M. clarkei* Williams (see Goldring 1923). Concomitant with the evolution of the ray trunks, the outer arms of a ray are gradually reduced and eventually lost. This is necessary to provide space for the proximal ramules of the ray trunks. One upper Devonian genus, *Trichotocrinus* (see Goldring 1923), went to the extreme of superimposing accessory ray trunks on the main ray trunks although this seems to have been an unsuccessful evolutionary experiment. At least some of these evolutionary changes are partially reflected in the ontogeny of melocrinitids such as *P. anglicus* and *Ctenocrinus paucidactylus* (Hall). The earliest specimens have four unbranched arms in each ray in which pinnules are lacking on the inner arms. This growth stage is known in *C. paucidactylus* but not in the promelocrinid. A similar phylogenetic stage with four arms in each ray is seen in *A. tetrarmatus* Brower and *G. decadactylus* although both the inner and outer arms bear pinnules. Throughout the ontogeny of *C. paucidactylus* and *P. anglicus*, new ramules are initiated as the ray trunks grow distally. Grossly similar changes are seen in the evolutionary sequence of *Promelocrinus* to *Ctenocrinus* to *Melocrinites*.

Brower (1974, pp. 33–44) discussed comparative ontogenies of camerate crinoids showing various types of brachials and arm-branching patterns, although quantitative data were not then available for forms with ray trunks. Consequently, the contrast between forms with and without ray trunks and hypertrophied arms will be emphasized. Note that both the exponents and the initial intercepts for the equations of *P. anglicus* are larger than those of the other crinoids (compare equations 1, 2 with 5–16 in Table 8). The slowest rates of growth of length of arms and number of brachials are found in the Ordovician *Eopatelliocrinus scyphogracilis* Brower, *E. latibrachiatus* Brower, 1973, and *Ptychocrinus fimbriatus* (Shumard) (see Brower 1973). All of these forms have two unbranched arms in each ray which consist of uniserial pinnulate brachials (equations 7–10, 15, 16, Table 8). Although none of these species are closely related to melocrinitids, the same configuration is seen in the ancestor of the Melocrinitidae, *G. ornatus*.

The acquisition of biserial brachials allows more brachials per unit length of arm because each side of the arm has a column of brachials. *Macrostylocrinus pristinus* Brower, has two unbranched biserial arms per ray which results in a more rapid rate of brachial addition relative to 'size' than seen in the eopatelliocrinids and *P. fimbriatus* (equations 11, 12, Table 8). Most advanced melocrinitids have biserial brachials as in *Promelocrinus anglicus* or compound brachials as found in some species of *Melocrinites* (compound brachials represent several biserial brachials which are fused together).

A. tetrarmatus Brower, a species with four unbranched arms in each ray that are composed of uniserial brachials, lies in the ancestry of *P. anglicus*. Note that the rate of development of new brachials and length of the arms is significantly slower than in *P. anglicus* (equations 5, 6, Table 8). This difference is directly correlated with the presence or absence of ray trunks and hypertrophied arms. *Ptychocrinus splendens* (Miller) (see Brower 1973) is a dicyclic camerate crinoid with uniserial arms which branch twice above the calyx, the branches being located on secundibrachs *13–15* and tertibrachs *30–40*. The half-rays of this form develop more rapidly relative to 'size' than in most camerates but the rate of growth is still slower than in *Promelocrinus anglicus* (equations 13, 14, Table 8).

In summary, the evolution of complexly ramified ray trunks or hypertrophied arms results in unusually rapid rates of development of new brachials and length of the arms. The rate of growth is roughly squared compared to idealized crinoids with simple arm configurations. Considering the food-gathering system only in terms of the arms and brachials is somewhat misleading because most of the plates and length of the food-gathering structures are represented by pinnules. In most camerates, over 95% of the total length of the food-gathering system is found in the pinnules (Brower 1973, 1974). Unfortunately, the length of and number of pinnulars in the average pinnule has only been measured for three specimens of *P. anglicus*; these data should be considered highly tentative and regarded with more than the proverbial grain of salt. Additional pinnules develop as new brachials are incorporated into the ramules and outer arms. Throughout ontogeny, new pinnulars form at the distal tips of the pinnules and the length of the pinnule is increased by the addition of new plates and calcite accretion on to old plates. The smallest crinoids, 'size' 5·5 mm, exhibit pinnules about 3·5 mm long which consist of about seven plates. The equivalent values for the largest crinoid from which data can be obtained, 'size' 13·7 mm, are 9·5 mm and twenty-three pinnulars. The equations are listed below.

$$(\text{Length of average pinnule}) = 0{\cdot}508\,(\text{`size'})^{1{\cdot}08}$$
$$(\text{Number of pinnulars in average pinnule}) = 0{\cdot}725\,(\text{`size'})^{1{\cdot}30}$$

About all the equations show is that the pinnules develop approximately isometrically with respect to size of the calyx. Brower obtained similar results for six species of Ordovician camerates (Brower 1974, pp. 35–37; Table 6 gives the exponents relative to calyx volume; these should be multiplied by 3·0 to give exponents with respect to a linear dimension such as 'size').

Growth of the entire food-gathering system. The number of plates and the length of the food-gathering system has been calculated for *P. anglicus* (equations 1, 2, Table 9). The data for the arms are taken from all 13 crinoids in the growth sequence. The figures for the pinnules are computed from the equations previously mentioned. The length of and the number of plates in the food-gathering system is a special type of a linear dimension which is in turn a sum and product of several other linear dimensions. The formulae are:

$$(\text{Total number of plates} = BR + BOA + (PP \times BOA) + (NR \times BAR) + (NR \times BAR \times PP)$$
$$(\text{Total length}) = LR + LOA + (BOA \times LP) + (NR \times LAR) + (NR \times BAR \times LP)$$

BR and *LR* are the number of brachials in and length of the ray trunk.
BOA and *LOA* are the number of brachials in and length of the outer arms.
BAR and *LAR* are the number of brachials in and length of the average ramule.
PP and *LP* are the number of pinnulars in and length of the average pinnule.
NR is the number of ramules.

The equation data are given in Table 9 for *P. anglicus* and a series of other species. In this case, the ideal exponent is 1·0 because all variables are linear dimensions. The main functions of the food-gathering system are to provide the viscera with food and to some extent oxygen. The gonads of camerates are presumably housed in the pinnules as in living crinoids. Extant comatulids also use the arms in moving from place to place by means of swimming and/or crawling although this does not seem to have been common in Paleozoic camerates.

The food-gathering capacity of a crinoid is largely controlled by two variables, firstly the number of plates, including both brachials and pinnulars, in the food-gathering system. This determines the number of food-gathering tube-feet (Brower 1973, p. 323; 1974, pp. 37–40). The second variable is the area drained by the food-gathering system which dictates the over-all size of the food-gathering system as well as the spacing of the food-catching tube-feet. Owing to geometrical complexity and preservation of the crinoids, the area usually cannot be measured and the length of the entire food-gathering system is used instead. Such is not unreasonable because the area comprises some function of length.

TABLE 9. Table giving equations for development of the entire food-gathering system relative to 'size' for *Promelocrinus anglicus* and other crinoids. Independent variable for all equations is 'size'. Equations 1 and 2 were fitted by the reduced major axis method whereas the others were done by least squares.

Equation number	Species	Dependent variable (y)	Initial intercept	Exponent	Minimum 'size' (x) mm	Predicted minimum y	Food-gathering ratio for smallest crinoid (y_{eq}/x_{obs})	Maximum 'size' (x) mm	Predicted maximum y	Food-gathering ratio for largest crinoid (y_{eq}/x_{obs})	Correlation coefficient	Standard error for slope
1	*Promelocrinus anglicus*	Total number of plates	14·3	3·26	5·5	37,300·0	6780·0	20·5	2,740,000	133,000·0	0·974	0·207
2	*Promelocrinus anglicus*	Total length in cm	8·49	3·10	5·5	1670·0	304·0	20·5	98,600	3250·0	0·970	0·208
3	*Alisocrinus tetrarmatus*	Total length in cm	5·88	2·88	1·1	7·73	7·03	6·7	1420	211·0	0·981	0·180
4	*Eopatelliocrinus scyphogracilis*	Total length in cm	6·40	2·25	1·15	8·77	7·62	7·7	631	82·0	0·926	0·246
5	*Eopatelliocrinus latibrachiatus*	Total length in cm	7·49	2·35	1·15	10·4	9·04	5·0	328	65·6	0·885	0·437
6	*Macrostylocrinus pristinus*	Total length in cm	4·35	2·98	1·0	4·35	4·35	7·0	1420	204·0	0·959	0·310
7	*Ptychocrinus splendens*	Total length in cm	10·3	2·07	2·1	47·7	22·7	12·7	1980	156·0	0·935	0·209
8	*Ptychocrinus fimbriatus*	Total length in cm	15·8	1·35	2·3	48·9	21·3	7·5	244	32·5	0·901	0·327

Thus crinoids are faced with the basic functional problem of most filter-feeding marine invertebrates. The food-gathering capacity is, at best, an area or (linear dimension)^2 function, but the tissue to be supplied with food is a volume or (linear dimension)^3 function. In *P. anglicus*, 'size' comprises the linear dimension and no attempt was made to estimate the volume of the calyx or tissue. However, the development of calyx volume relative to 'size' in various Palaeozoic camerates closely follows a cubed function (Brower 1973, 1974).

Several tentative conclusions can be drawn from the table (see also discussion in Brower 1973, p. 319; 1974, pp. 33–44).

1. In general crinoids with pinnulate arms seem to have maximized the growth rates of the length and number of plates in the food-gathering system with respect to size and tissue volume as much as possible within the inherent geometrical limits of the food-gathering system. Except for *Ptychocrinus fimbriatus*, the food-gathering system develops much more rapidly than one would predict based on the ideal case (Table 9).
2. Of all crinoids listed in Table 9, *Promelocrinus anglicus* is characterized by the most rapid rate of growth of the food-gathering system. This is dictated by the interaction of the large exponents and high initial intercepts. For example, both *Macrostylocrinus pristinus* and *A. tetrarmatus* are characterized by large exponents which are only slightly less than in the promelocrinid; however, the initial intercepts of these two species are significantly smaller than in *P. anglicus* which dictates a slower rate of growth of the food-gathering system. In most of the other species, the exponents are much lower than those of *P. anglicus*. This situation is attributed to the acquisition of ray trunks and hypertrophied arms. None of the other species exhibit hypertrophied arms; all have normal patterns of arm branching. Brower (1973, pp. 318–324; 1974, pp. 34–40; see also previous material on the arms) presented discussions of ontogeny of all species except *P. anglicus*.
3. The 'food-gathering ratio' equals [(length of food-gathering system) or (number of plates in food-gathering system) or (number of food-catching tube-feet)]/[(calyx volume) or (volume of tissue)]. *P. anglicus* shows isometry or positive allometry of the food-gathering system relative to tissue volume; consequently the food-gathering ratios either increase or remain constant throughout ontogeny (I assume the tissue volume or calyx volume increases roughly as ('size')^3 during growth). All other species which I have investigated, and probably most camerate crinoids, are characterized by more or less striking negative allometry and the food-gathering ratios decline in older and larger crinoids (Table 9 lists data for growth of the food-gathering system relative to 'size' but this is better seen in the equations with respect to calyx volume given by Brower 1973, pp. 319–323; 1974, pp. 37–40, Table 7).

Continuation of this ontogenetic pattern could produce a 'hypothetical crinoid' where the number of food-catching tube-feet is too low and the food-gathering system too short to provide the volume of soft tissues with food. Obviously no crinoid reached this critical limit although some forms may have approached it. Perhaps some ratio of [(length of the food-gathering system)/(tissue volume)] or [(number of food-catching tube-feet)/(tissue volume)] serves as a limit beyond which further increase of tissue cannot take place. The achievement of isometry or positive allometry in *P. anglicus* circumvents this particular size limitation. This may be partially reflected in the 'sizes' of the largest adults of the species listed in Table 9. *P. anglicus* is by far the largest form, maximum 'size' being 20·5 mm versus 5·0–12·7 mm. I concede that there are alternative explanations for the differences in 'sizes' which may be equally likely (Brower 1973, pp. 325, 326; 1974, pp. 44–46).

The filtration net. To consider *P. anglicus* and other melocrinitids only in the context of the number of food-catching tube-feet is somewhat misleading. Crinoids trap their food by means of filtration nets which are formed by the arms and pinnules. Melocrinitids probably engaged in full mucus net feeding like most adult crinoids of the Recent (Lane and Breimer 1974). Depending on the environment, the filtration net can be orientated in one of two ways (Breimer 1969). In quiet water conditions the food supply consists of a vertical rain of plankton and/or organic detritus. The stem is erect and the arms are spread horizontally to form a collecting bowl. When current or wave action is present, at least part of the food travels parallel to the substrate. The stem is flexed and bent with the current. In this case, the food-gathering system forms a vertically orientated filtration net. Regardless of environment, the basic orientation of the filtration network is at right angles to the direction of food transport.

Text-fig. 6 illustrates schematic plan views of the filtration networks of two crinoids. The most primitive form, *Glyptocrinus ornatus* has ten unbranched arms. The primitive filtration net is incomplete because there are large gaps between the pinnules of adjacent arms and rays. Several specimens of *Promelocrinus* are preserved with the arms in the spread or food-gathering orientation and these individuals allow reconstruction of the filtration net (e.g. text-fig. 4). Typically, the crinoids were buried with the arms in the partially closed (e.g. Pl. 100, fig. 4) or in the fully closed or resting position (e.g. Pl. 100, fig. 1). In *P. anglicus*, the filtration network is complete and covers the entire perimeter of the arms. There are no large spaces between the adjacent arms and pinnules. Here, almost all food particles flowing through the arms and pinnules would be filtered. The pinnules are too long to fit between the ramules and the outer arms; consequently, these must face distally and outward from the plane

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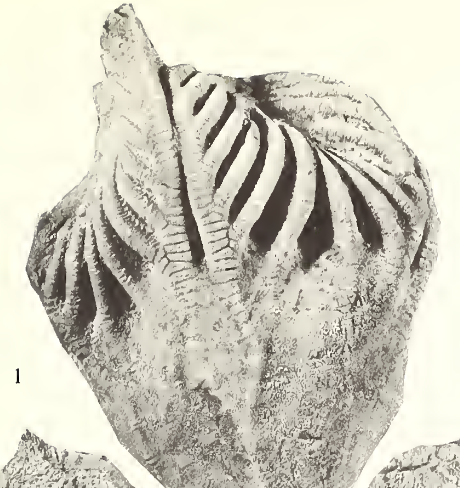
EXPLANATION OF PLATE 102

Figs. 1, 2, 4. *Promelocrinus anglicus* Jaekel. 1, lateral view of SM. A12767, note relatively small arms, complete intersecundibrachial areas, granulose calyx plates with raised margins. 2, lateral view of S. 271, a complete crown with fifteen ramules and crushed calyx, × 1·25. 4, stem segment of SM. A10136, a syntype of *Mariacrinus flabellatus* Salter, the stem segment closely resembles those found attached to crowns of *Promelocrinus anglicus* and this specimen is assigned here with little doubt.

Figs. 3, 5. Specimens assigned by Salter to *Mariacrinus flabellatus* for unknown reasons, I have not seen any such material associated with *Promelocrinus anglicus* and these specimens are unidentified here. 3, SM. A12759, cirrus root lying on a bedding plane, apparently the crinoid was uprooted when burial took place, burial was probably rapid and possibly by mudflow, the living orientation of such cirrus roots which have cirri on all sides is with the axis of the stem vertical. 5, SM. A12761, massive distal stem segment or rooting device with cirri.

All figures × 1·5 unless otherwise stated.



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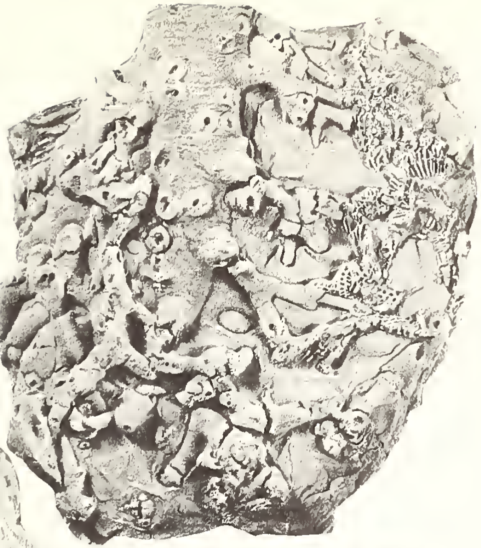

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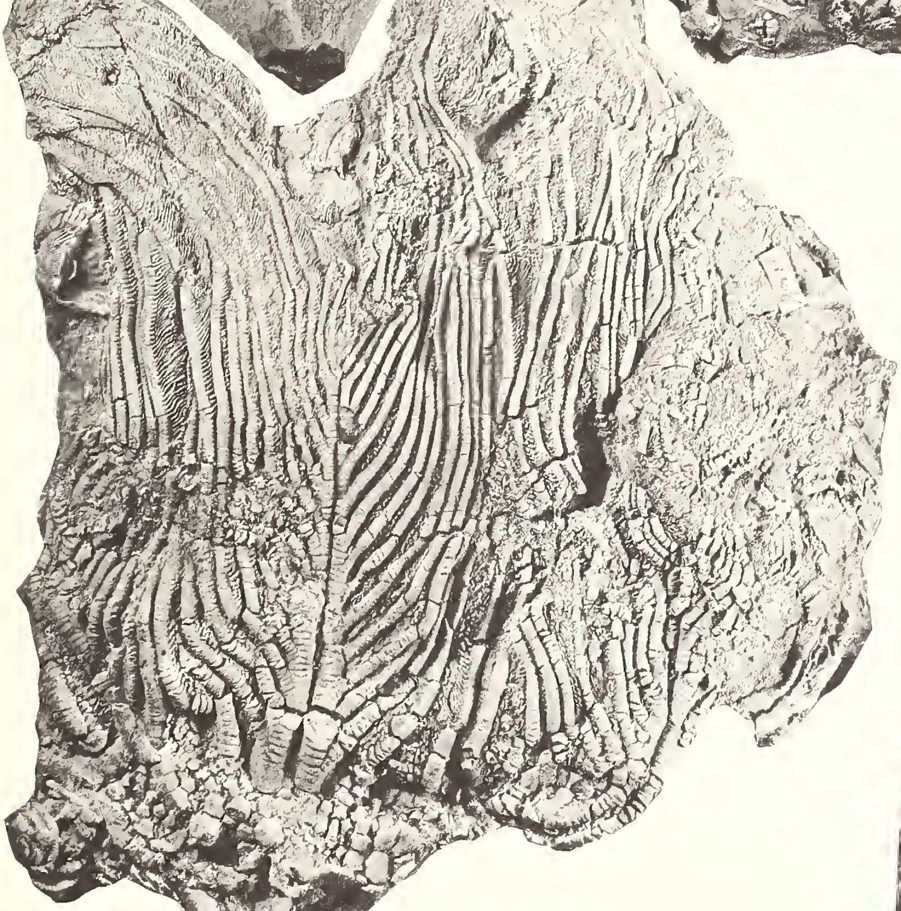

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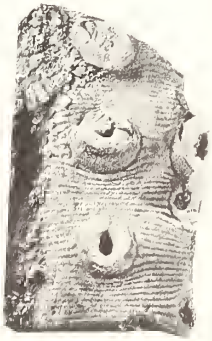

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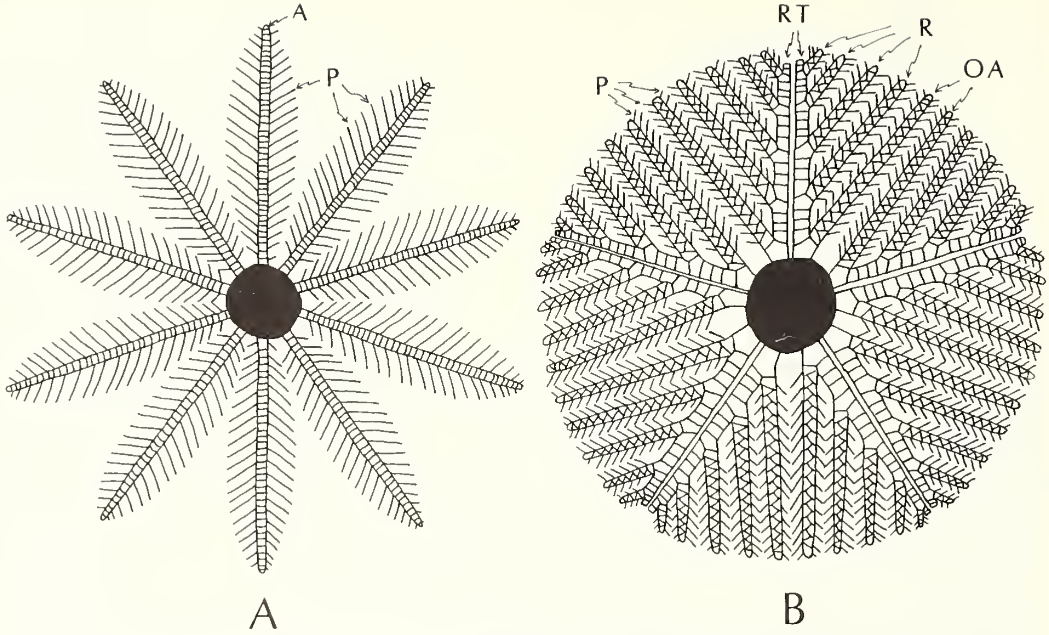
BROWER, Wenlock crinoids



TEXT-FIG. 6. Schematic sketches of plan views for filtration nets of *Promelocrinus* and ancestor, not to any scale. A, *Glyptocrinus ornatus* Billings, note gaps in the filtration net between the arms. B, *Promelocrinus anglicus* Jaekel, the filtration net is complete, only a few ramules are shown in order to simplify the drawing. Symbols: P = pinnules; A = arms in *Glyptocrinus*; RT, R, and OA denote ray trunks, ramules, and outer arms respectively in *Promelocrinus*.

of the arms. One might note that the evolution of ray trunks or hypertrophied arms commonly produces a complete filtration net. This is clearly seen in melocrinitids and in various unrelated crinoids which also developed ray trunks such as *Lamptero-crinus* (see Springer 1926), *Cytidocrinus* (see Wachsmuth and Springer 1897), and *Manillacrinus* (Campbell and Bein 1971).

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A NEW GENUS OF CALCEOCRINID FROM SPAIN WITH COMMENTS ON MOSAIC EVOLUTION

by G. D. WEBSTER

ABSTRACT. *Espanocrinus lemonei* n. gen., n. sp. is the first calceocrinid crinoid reported from the Early Devonian of Spain. This genus has primitive main axil and arm structure and advanced dorsal cup features. This suggests that mosaic evolution occurred in the calceocrinids and that cup changes were most significant in Ordovician to Devonian time. Modifications of the main axil and arm were thereafter most important in some lineages.

DURING the 10th International Field Institute, sponsored by the American Geological Institute, a visit was made to the Devonian section on the west cape of the Bay of Arnao, near Aviles (Asturias), Spain. The geologic section there consists of interbedded grey limestones and red shales of Early Devonian (Emsian) age thrust over Late Carboniferous (Westphalian) clastics. The limestones, which contain abundant specimens of *Trybliocrinus flatheanus* (Geinitz 1867), are correlated by Comte (1959) to the La Vid Shale and considered to be of early Emsian age.

While studying the *T. flatheanus* beds a calceocrinid was discovered by Dr. David LeMone who generously turned the specimen over to me for further investigation. That specimen is the first known calceocrinid from Spain and adds to the known evolutionary morphology and geographic distribution of this unique group of crinoids.

The calceocrinids are a unique family of the inadunate crinoids. Their primary distinguishing features are the possession of pronounced E ray bilateral symmetry and a transverse hinge crossing the cup beneath the E inferradial. The crowns are generally slender and elongate. The E ray arm is more robust than all others. In the enclosed position the crown commonly folds down against the proximal stem. Their greatest diversity occurred in the Devonian after which they declined rapidly to a rather small segment of crinoid faunas. Calceocrinids persisted until Early Permian time.

Morphologic terms used in the accompanying description follow those proposed by Moore (1962) and Moore and Strimple (1973).

SYSTEMATIC PALAEONTOLOGY

Subclass INADUNATA Wachsmuth and Springer, 1885
Order DISPARIDA Moore and Laudon, 1943
Superfamily HOMOCRINIDAE Ubaghs, 1953
Family CALCEOCRINIDAE Meek and Worthen, 1869
Genus *Espanocrinus*, n. gen.

Diagnosis. A calceocrinid with perfect bilateral symmetry, weakly gaped hinge, adjoined large radials; three basals, DE and EA basals fused into adanally convex

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triangular plate, AB and CD basals rectilinear sharing stem attachment; prominently protruded anal tube at base of crown; undivided median arm; 6 axial arms, 3 each side; 4 main axil plates, only second and fourth axillary with largest branch always abanal.

Description. See the following description of the type species and plate diagram (text-fig. 1).

Type species. E. lemonei.

Espanocrinus lemonei, n. gen., n. sp.

Plate 103; text-figs. 1–2

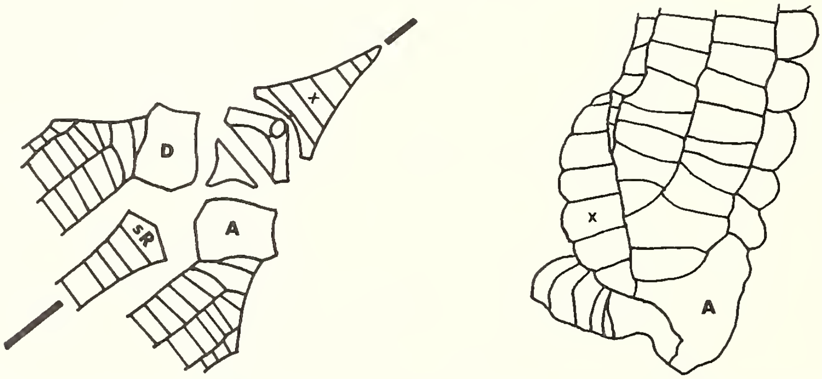
Material. One crown, to be deposited in the U.S. National Museum, Smithsonian Institution, USNM 221559.

Diagnosis. As for the genus.

Description. Crown: perfect bilateral symmetry, slender, elongate, gently curved adanal distally; length 80·5 mm curved, 87·7 mm along curvature, most distal brachial lacking; width at hinge slightly incomplete 12·4 mm, at large radials 12·0 mm, at IBr_{10} of median ray 8·2 mm, at distal tip 4·4 mm; depth at maximum through IBr_1 of median ray to tp_3 14·7 mm, at IBr_{10} of median ray 10·7 mm, at distal tip 3·6 mm.

Cup: higher than wide in median ray view, sharply constricted above hinge on sides of large radials, tapers moderately toward median ray on distal tip of large radial and across lateral edges of superradial of median ray; triangular in basal view, greatest dimension along hinge line; maximum height 12·2 mm, maximum width through large radials 12·0 mm; in enclosed position basal surface makes a right angle with base of median ray surface.

Basals: three; EA–DE basals fused into a single convex subtriangular plate, straight along hinge line, 7·5 mm long, convex adanally, 4·0 mm wide, slightly more triangular appearing than crescent-shaped in outline; AB and CD basals mirror images, both appear somewhat dumb-bell-shaped, larger on the ends and constricted



TEXT-FIG. 1. *Left*, plate diagram of *Espanocrinus*, n. gen., diagrammatic, based on holotype. Plane of symmetry indicated by heavy diagonal line; X, primanal; A and D, radials; sR, E ray superradial. *Right*, *E. lemonei*, n. gen., n. sp., right anterior view of holotype, taken from inked bleached photograph (×2).

in the centre, concave exterior, adjoin large radial abanally, enclose DE–EA basal adanally, mutually share stem attachment, maximum width 9·0 mm, height at stem attachment 3·9 mm, at central constriction 2·7 mm, at slightly incomplete hinge end 4·5 mm. In retracted position the AB and CD basals touch against the A radial–B inferradial and D radial–C inferradial respectively; in expanded position B and C radials would not be in contact with AB and CD basals respectively.

Radials: large A (anterior) and D (left posterior) radials mirror images, sideways V-shaped in median ray view caused by constriction between hinge bulge at base and outflaring of distal two-fifths of plate with gently inward bending of distal tip, constriction sharp enough to appear as a suture on sides of cup but not on the median ray side, A radial bounded in a clockwise direction by E superradial, D radial, E inferradial, AD basal, B inferradial, IBr_1, and IBr_2; height 9·8 mm, width 7·2 mm, A and D radials mutual suture 2·1 mm long; small inverted T-shaped E inferradial with concave sides where adjoined to radials, hinge slightly deformed, height 4·8 mm, width 8·2 mm, A and D mutual suture 2·1 mm; E superradial convex proximally and adanally, moderately inflated transversely on exterior, moderately concave distal surface, width at base 9·6 mm, width at top 8·0 mm, midheight 3·0 mm, slight proximal flare on proximal lateral edge; B and C inferradials triangular in outline, partly covered by proximal stem segments, possibly but doubtfully fused into one plate, probably have a mutual groove or impression that the proximal three or four stem segments fit into when crown is in the enclosed position, concave distal surfaces; subanal (B–C superradial) one fused plate, moderately convex proximal surface, gently concave distal surface, strongly protruded exterior surface, twice as wide as high; primanal immediately above subanal and of same protruding shape, slightly distorted in preservation, followed by four tube plates each decreasing in size to the small half-conical pointed fourth one, all strongly protruded exteriorly.

Arms: seven, elongate, unbranched. E ray brachials wider than high, strongly bulbous but more so transversely than laterally, slight flange along lateral edges with adjoining arms, IBr_1 9·0 mm wide, 3·0 mm high; IBr_2 7·0 mm wide, 3·9 mm high; IBr_{10} 6·6 mm wide, 3·7 mm high; IBr_{20} 4·5 mm wide, 3·3 mm high. Main axils four in each lateral ray only two of which in each ray are axillary; main axil I non-axillary, wedge-shaped pointed abanally, convex proximal surface, planar distal surface; main axil II axillary, wider branch abanally, approximately twice as wide as high, planar proximal surface, gently concave branching surfaces; main axil III non-axillary, wedge-shaped, pointed abanally, gently convex proximal and distal surfaces, approximately two-fifths as high as wide; main axil IV axillary, much wider branch abanally, gently concave proximal surface and moderately convex distal surface. Six lateral or axil arms, three each side, unbranched thus each composed only of alpha brachial, largest abanal, central one only slightly smaller than abanal one, adanal ones (omega) markedly smaller not reaching apex of crown, left posterior omega arm two-thirds shorter than A ray omega arm; centrally elevated ridge extending length of arms, producing a ribbed appearance to the crown, faint flange on lateral edges of brachials.

Stem round, axial canal round, column tapers distally; proximal five columnals preserved; diameter of proximal columnal 4·7 mm, diameter of fifth columnal 4·1 mm.

Remarks. The symmetry and cup structure of *Espanocrinus lemonei* show advanced evolutionary features of the Calceocrinidae. That is, the symmetry is perfectly bilateral, the A and D radials are adjoined separating the E inferradial and superradial, the DE and EA basals are fused into one plate, the B and C inferradials are in contact, and the stem is moved back, attaching on to the AB and CD basals only. All these features are found also in *Halysiocrinus*. The structure of the main axils is primitive in that there is a non-axillary main axil below each axil; this is common in *Calceocrinus*, *Cremacrinus*, and *Anulocrinus*, the three oldest known genera of the family. In addition, the lack of branching on the median and axil arms is considered primitive, as is the small number of arms. Thus, both advanced and primitive features are found on *Espanocrinus*, as might be expected of a calceocrinid occurring near the midrange (Early Devonian) of the time span of the family (Middle Ordovician–Early Permian).

A comparison between *Espanocrinus* and previously described calceocrinid genera strongly suggests that mosaic evolution took place in the calceocrinids. It clearly shows that, at the generic level, different parts of the crown were evolving at different rates. Evolution of the cup was exceedingly important in the Ordovician, Silurian, and Early Devonian, as pointed out by Kesling and Sigler (1969). In Middle Devonian to Permian time, changes were still occurring in the cup but they appear to be less significant than changes in the main axils, anal tube, and arms. Thus advanced configuration of the cup plates preceded modifications in the main axils and arms. This is undoubtedly related to the function of the animal and may reflect a modification in feeding habit or environment.

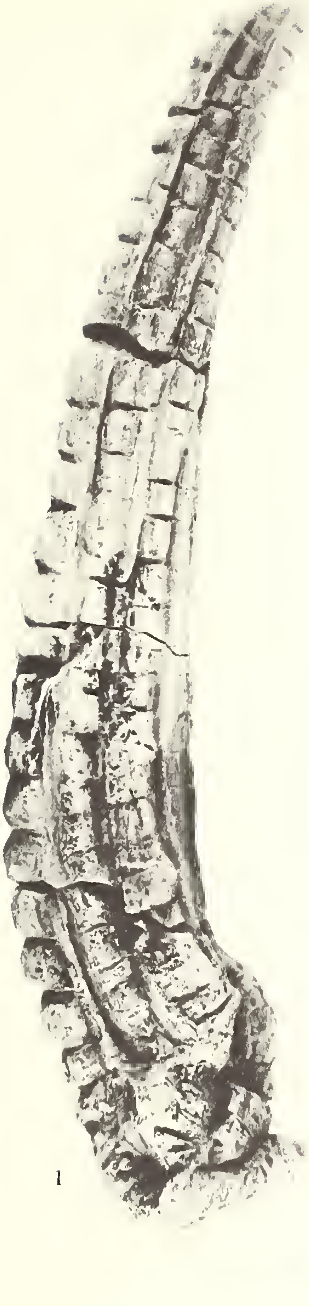
Two genera of calceocrinids, *Eohalysiocrinus* and *Halysiocrinus*, are closely allied to *Espanocrinus* in the structure of the cup. *Eohalysiocrinus* is a small form in which the main axils are not developed, and the C and B inferradials are very short (Prokop 1970). This contrasts with the poor to moderate development of the main axils and longer C and B inferradials on *Espanocrinus*. The position of the columnar facet is shared on the AB and CD basals, tangent to the third basal, in *Espanocrinus*; in *Eohalysiocrinus* the same condition may exist or the stem facet may be shared by all three basals. *Halysiocrinus* differs in having highly developed main axils and the stem facet restricted to the AB and CD basals.

Because the cup plate arrangement of *Espanocrinus* is so similar to that of *Halysiocrinus*, a careful review of the species assigned to the latter genus was made. This review of the thirteen species assigned to *Halysiocrinus* by Moore (1962) and Brower (1966) revealed that three are of Middle Devonian age and ten are of Early Mississippian age.

The three Middle Devonian species have strongly protruding anal tubes at the base of the crown, as in *Espanocrinus*, but seven to ten branching axil arms on each side of the cup, whereas *Espanocrinus* has only three unbranching axil arms. I believe that these three forms represent a new genus of calceocrinid.

EXPLANATION OF PLATE 103

Figs. 1–4. Holotype of *Espanocrinus lemonei*, n. gen., n. sp. 1, left posterior view; 2, median view; 3, right anterior view; 4, basal view. All views ×2.



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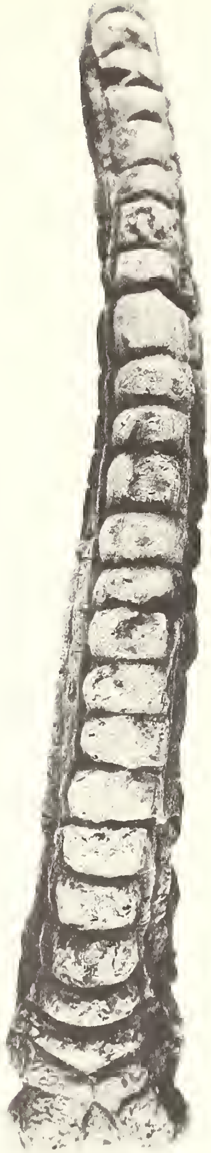

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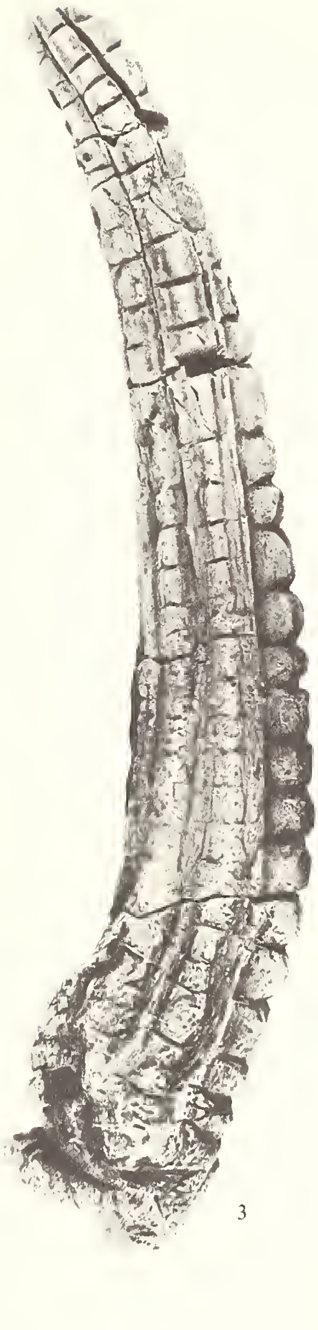

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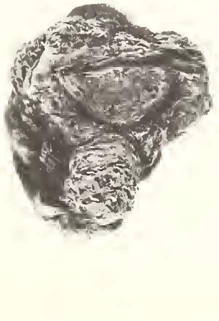


WEBSTER, Calceocrinid from Spain

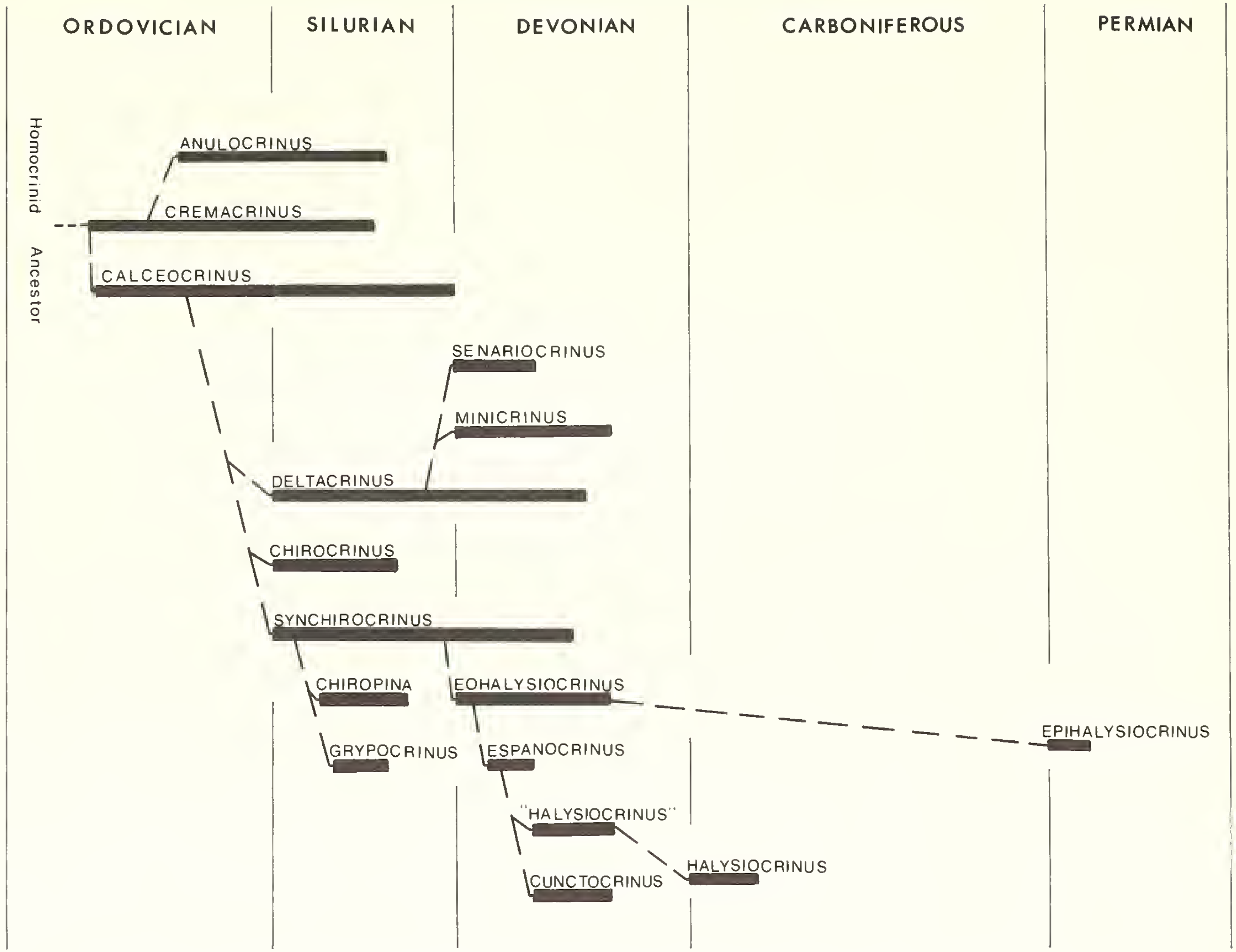
The ten Early Mississippian species assigned to *Halysiocrinus* include the type species *H. dactylus* Hall, 1860, and also *H.? lamellosus* (Hall, 1860), a *nomen nudum* based on an undescribed, unillustrated set of arms. The remaining nine species show two cup shapes. One is relatively elongate, high enough to have a gap between the column and the main axils when the cup is enclosed and the hinge forms a right angle in the enclosed position. The second has a relatively low cup, and in the enclosed position the column is against the main axils and the hinge forms an acute angle. In addition, the Mississippian species of *Halysiocrinus* lack, or have a very small, protruding anal tube at the base of the crown, and the arms enshroud the anal tube. They generally have four or five branching axil arms—the reported acutal range is three (*H. bradleyi* (Meek and Worthen, 1860)) to seven (*H. nodosus* (Hall, 1860) has from five to seven axil arms). I consider both *H. nodosus* and *H. robustus* (Worthen, 1890) to be junior synonyms of *H. tunicatus* (Hall, 1860).

Thus Mississippian species of *Halysiocrinus* have more axil arms than *Espanocrinus* but generally fewer than Devonian species of *Halysiocrinus*, and they lack the prominent anal tube found in *Espanocrinus* and the Devonian forms. In addition, *Espanocrinus* has one non-axillary main axil below each axillary (text-fig. 2). Only two species of the Devonian and Mississippian halysiocrinids have non-axillary main axils; these are *H. elephantinus* Laudon, 1936 (Devonian) which has only main axil I_1 non-axillary, whereas *H. springeri* Brower, 1966 (Mississippian) has main axil I_1 and II_1 non-axillary but no others.

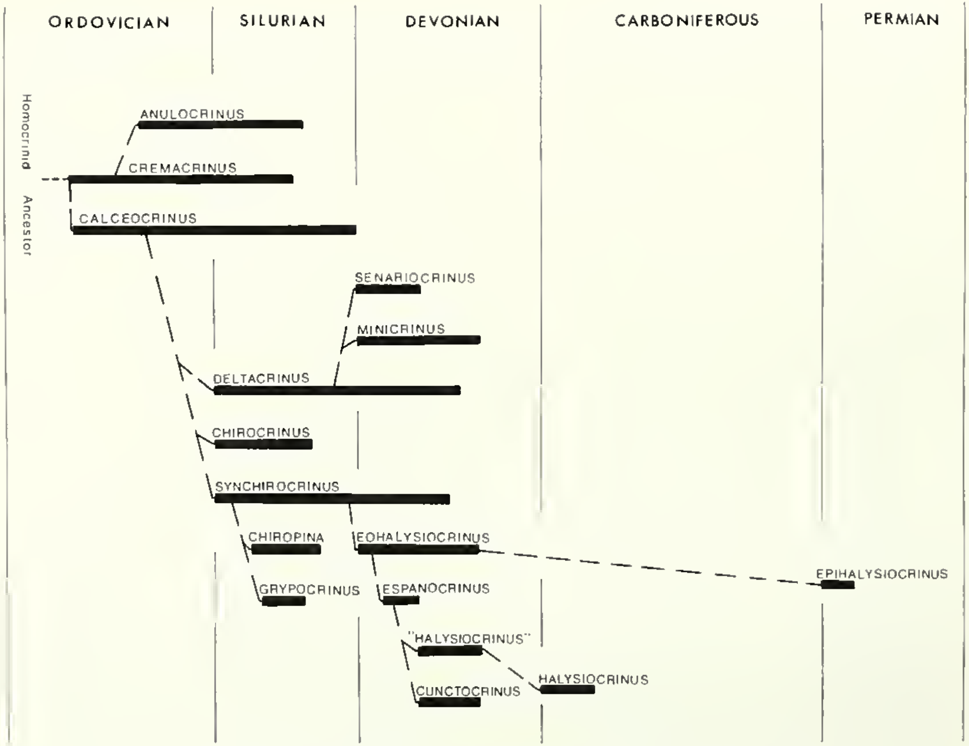
In all calceocrinids, except *Espanocrinus*, the adanal is the longest of the branching sutures of any axillary main axil, and the abanal is the shortest, except that the reverse condition is found in the last or omega ramule branch. In *Espanocrinus* the longest suture is always the abanal one.

Brower (1966) suggested that *Halysiocrinus* was possibly derived from *Deltacrinus*, pointing out the similarity of arm branching and separation of the E ray inferradials and superradials. Moore (1962) interpreted *Deltacrinus* and *Halysiocrinus* as descendants of *Calceocrinus*. However, he believed that the Ordovician to Early Devonian forerunners of *Halysiocrinus* were unknown. *Espanocrinus* fills the Early Devonian gap in this lineage. It is not thought to have evolved from *Deltacrinus*, because of the moderate development of the unbranched main axils. The three Middle Devonian species of *Halysiocrinus* were probably derived from *Espanocrinus* and in turn gave rise to the Early Mississippian halysiocrinid species.

The phylogeny of the calceocrinids has been discussed by several authors recently. Prokop (1970, fig. 19) followed the phylogeny of Moore (1962, fig. 21) with slight modifications. Kesling and Sigler (1969, fig. 10) and Rowell (1969, fig. 2) approached the phylogeny from two numerical taxonomic methods that resulted in moderately similar phylogenies which differ significantly from that of Moore (1962). Some difficulties are noted in these phylogenies when time is considered. Rowell (1969) shows *Chirocrinus* (Early–Middle Silurian) and *Synchirocrinus* (Early Silurian–Middle Devonian) as derived from *Grypocrinus* (Middle Silurian). Kesling and Sigler (1969) and Rowell (1969) show *Seniocrinus* (Early Devonian) derived through *Cunctocrinus* (Middle Devonian) from *Halysiocrinus* (Middle Devonian–Early Mississippian). Rowell (1969, p. 232) noted that the spacing in his fig. 2 for *Senariocrinus* was equidistant from *Deltacrinus* (Early Silurian–Middle Devonian) and



TEXT-FIG. 2. Stratigraphic distribution and inferred phylogenetic relationships of the genera of the Calceocrinidae.



TEXT-FIG. 2. Stratigraphic distribution and inferred phylogenetic relationships of the genera of the Calceocrinidae.

Cunctocrinus (Middle Devonian) and that he was showing *Senariocrinus* to lead to *Cunctocrinus*. These inconsistencies may reflect our incomplete knowledge of the geologic and geographic distributions of the calceocrinids. They certainly point out our incomplete record if the geologic ranges of known genera are valid and are not modified in the future. A suggested phylogeny based on Kesling and Sigler's (1969) work, that incorporates genera named since then, is shown in text-fig. 3.

Breimer (1962) described the species of Devonian crinoids from Spain and recorded their known occurrences. Crinoids previously reported from the Bay of Arnao locality and found in association with *E. lemonei* are *Stamnocrinus intrastigmatus* (Schmidt, 1932) and *Trybliocrinus flatheanus* (Geinitz, 1867). Specimens of *T. flatheanus* (often incorrectly referred to by its junior synonym *Hadrocrinus hispanae*) are exceedingly abundant at this locality and (also because of their size and excellent preservation) overshadow the remaining fauna.

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DISTINCTION BETWEEN SYMPATRIC SPECIES OF *MICRASTER* (ECHINOIDEA) FROM THE ENGLISH CHALK

by ROBERT B. STOKES

ABSTRACT. Sympatric species of *Micraster* recorded from the upper Cretaceous Chalk of England are most easily distinguished from one another by the relative height of their periprocts measured from the base of the test. The observation of Gauthier (1887) and Melville (1954) that *Micraster* species with a high conical aboral surface (so-called 'gibbous' forms) have a lower periproct than the associated non-gibbous forms is confirmed by numerical analysis of samples from the Santonian of Kent (*M. gibbus* and *M. coranguinum*) and the upper Campanian of Norfolk (*M. stolleyi* and the *M. schroederi–glyphus* lineage). The nomenclature of the gibbous species *M. gibbus* and *M. stolleyi* is discussed.

THE genus *Micraster*, which ranges from middle Turonian to lower Maastrichtian, is often represented by a pair of sympatric species consisting of a gibbous species (i.e. one with a high conical aboral surface), and a non-gibbous species.

Throughout most of the nineteenth century all gibbous species were referred to *M. gibbus* (Lamarck, 1816). Whilst usually placed in the genus *Micraster*, Lamarck's species was sometimes regarded as an *Epiaster* (e.g. by Schlüter 1869 and Wright 1878), because of the absence of fascioles on many specimens.

Gauthier (1887) insisted that these gibbous forms be replaced in the genus *Micraster* and emphasized that their most obvious characteristics are the conical shape, the length of the petals, and the low periproct. He also noted that the pores of the unpaired petal are conjugate like those of the paired petals (in contrast with non-gibbous forms in which they are round and in which pores of one pair are separated by granules) and that the subanal fasciole may be present, reduced, or absent (in contrast with non-gibbous forms in which it is always present). In his discussion of *M. gibbus*, Gauthier suggested that the name *Gibbaster* might be used for the gibbous species but he did not designate a type-species for this new genus.

Lambert (1895, 1901, 1911) consistently omitted shape as a characteristic of *Gibbaster* and restricted this name to forms which have a subanal fasciole and conjugate pores in the unpaired petal, *M. fastigatus* Gauthier being designated as type species by Lambert and Thiéry (1924). The latter authors diagnosed *Isomicraster* Lambert, 1901 as having conjugate pores in the unpaired petal and lacking a subanal fasciole and designated *I. stolleyi* Lambert as the type species. Whilst these two taxa (regarded by Lambert and Thiéry as subgenera of *Micraster*) include all the gibbous species, since the shape of the test is no longer a diagnostic feature, non-gibbous *Micraster* with conjugate pores in the unpaired petal could be placed in *Gibbaster*. This has happened in the case of *G. belgicus* Lambert, 1911, the broad flat holotype of which I regard as a typical *M. rogalae*. I therefore reject the use of the nature of the pores in the unpaired petal as a criterion for subdividing the genus *Micraster*.

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Most modern workers (e.g. Mortensen 1950; Fischer 1966) have followed Lambert in attaching great importance to the presence or absence of fascioles and have, as Kermack (1954) pointed out, been forced to remove *Isomicraster* from the family Micrasteridae and place it in the Toxasteridae. Having followed Mortensen in such a classification, Fischer (1966) concluded that the micrasterids were derived from the toxasterids via *Isomicraster* even though stratigraphical occurrence does not allow such a phylogeny and Kermack (1954) had shown that *Isomicraster* were evolved from *Micraster* by the disappearance of the fasciole due to natural selection. I wholeheartedly agree with Kermack's statement (1954, p. 421) that 'The presence or absence of a fasciole is therefore a most unsuitable character upon which to build the major subdivisions of the amphisternous spatangoids'. Within the genus *Micraster* a subanal fasciole is often present on specimens of species which have usually been placed in *Isomicraster*: e.g. *M. gibbus* (= *M.* (*Isomicraster*) *senonensis* in Kermack 1954) and *M. stolleyi* (R. V. Melville quoted in Mortensen 1951, Nichols 1959). The presence or absence of a subanal fasciole is therefore rejected as a means of distinguishing between sympatric species of *Micraster*.

This paper advocates a return to the views of Gauthier (1887) according to which gibbous *Micraster* are most easily distinguished from non-gibbous species not only by their conical shape but also by the low position of the periproct. Numerical data, derived from samples of gibbous and non-gibbous species collected from the same stratigraphical horizons, are recorded below in support of this assertion.

Method. The height of the highest part of the test (= total height) and the height of the top of the periproct were measured from the base of the test using a microball height gauge calibrated to an accuracy of 0·005 inches (0·002 mm). The instrument and the specimen being measured were placed on a sheet of ground glass so that the base of the height gauge corresponded to the base of the test. As both measurements were taken along the same axis, slight distortion of the specimens does not substantially affect the periproct height ratio (height of the top of the periproct: total height).

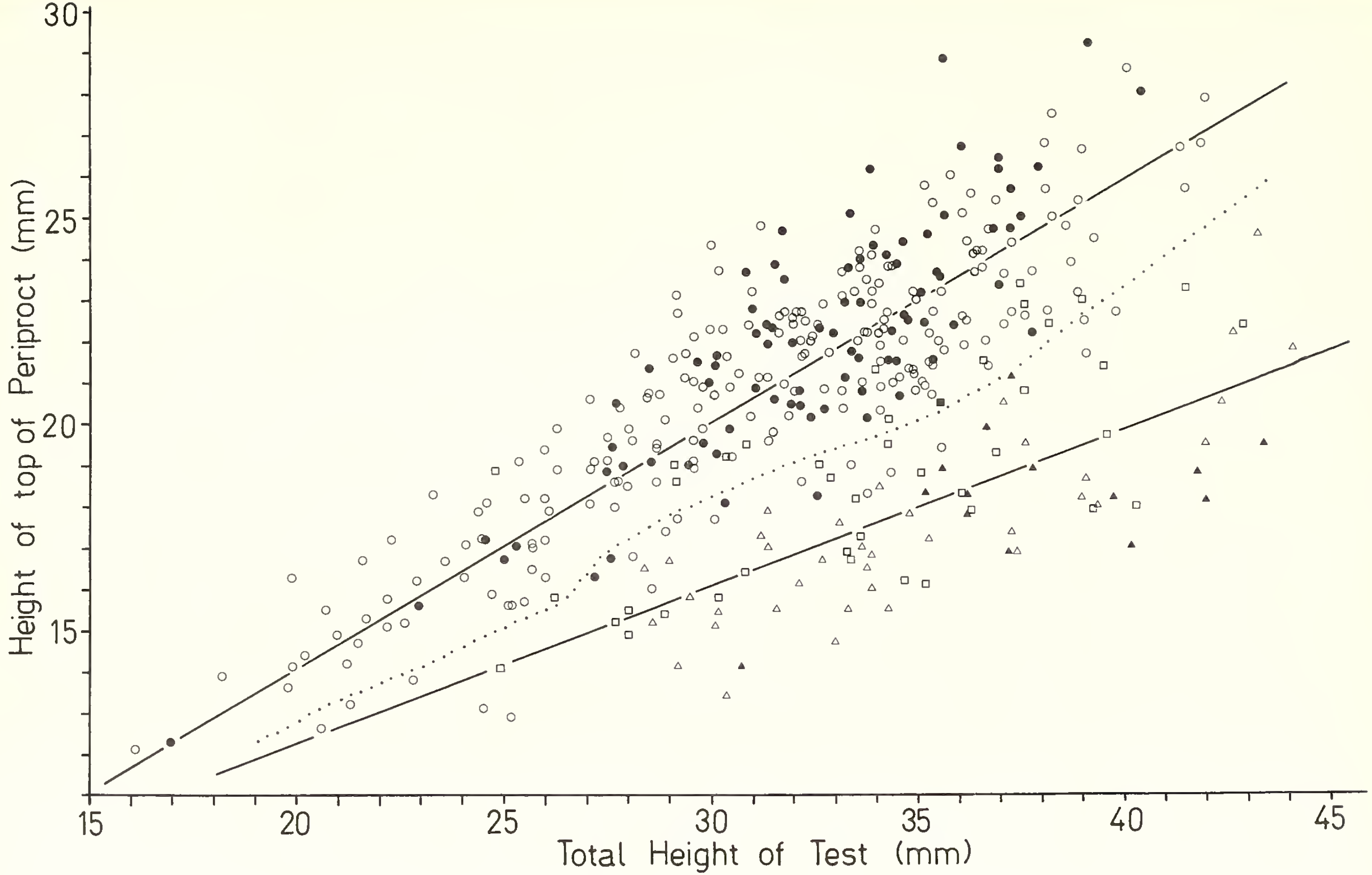
The original data is deposited in the Echinoderm Section, Department of Palaeontology, British Museum (Natural History).

M. GIBBUS AND *M. CORANGUINUM* FROM THE SANTONIAN OF KENT

Material. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent, now in the British Museum (Natural History). The 516 specimens which form this collection were purchased by Rowe from workers in the local quarry (? quarries) at Northfleet and thus it is impossible to give a more precise definition of the horizon(s) from which they came. The use of such a sample is justified because *M. gibbus* is such a rare species that no collection from accurately known horizons contains it in statistically acceptable numbers and, since this is the same sample which Kermack (1954) studied so thoroughly, the data presented below can be compared with, and supplement, Kermack's results and conclusions. The validity of the Northfleet sample in relation to 'populations' of fossils embedded in the chalk and the succession of living populations of which it represents the remains has been fully discussed by Kermack (1954).

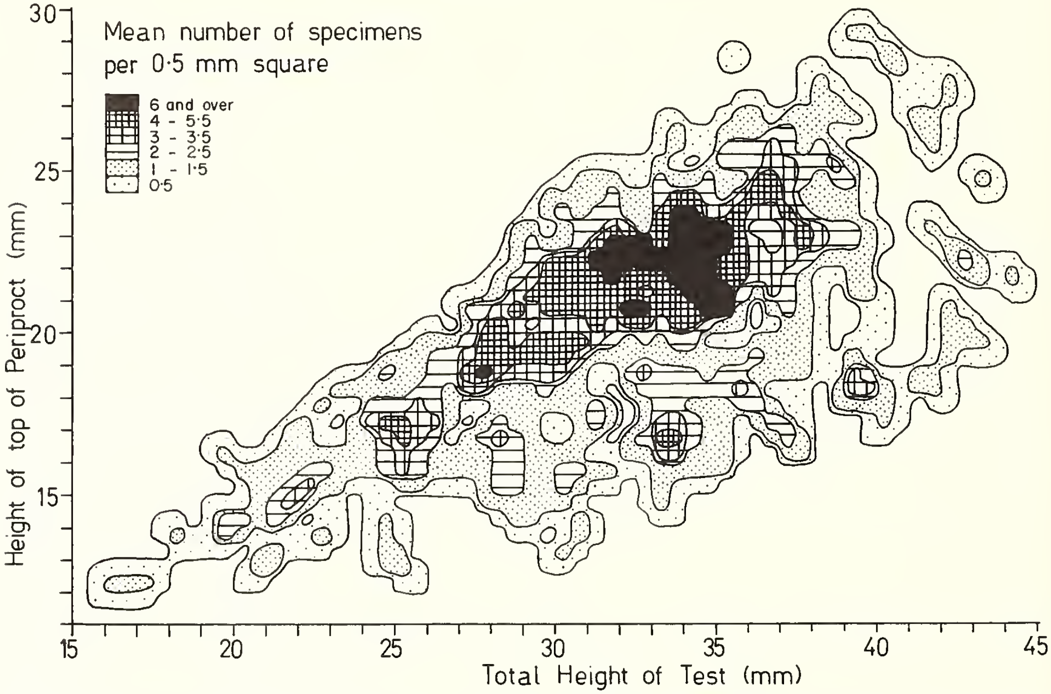
The two measurements could be taken on only 392 of the specimens but I measured only the height of the top of the periproct and used Kermack's (1950) measurements of the total height. Any error introduced by the acceptance of Kermack's measurements will be systematic and will have no significant effect on the graphs or the periproct height ratio.

Results and conclusions. Text-fig. 1 shows a simple plot of the measurements, the different symbols indicating Rowe's manuscript divisions of the sample. The presence



TEXT-FIG. 1. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent. The following manuscript divisions of Rowe are represented: open circles = '*M. coranguinum* (Leske)'; black circles = '*M. coranguinum* (Leske) var. *latior*'; black squares = '*M. coranguinum* in all respects, save that there is no fasciole'; open squares = '*M. coranguinum* nearing *Epiaster* shape, but in no other way resembling it' plus '*M. coranguinum* still nearer to *Epiaster* shape, but in no other way resembling it'; open triangles = '*M. coranguinum* nearing or actually reaching *Epiaster* shape, and having a feebly developed fasciole' plus '*M. coranguinum* with anterior ambulacrum in process of modification, and the shape of *Epiaster* but with a slight but definite fasciole' plus '*Epiaster gibbus* save for the anterior ambulacrum'; black triangles = '*Epiaster gibbus*'. See text for further explanation.

of two species becomes evident only in text-fig. 2, which shows the density of the distribution of the specimens in text-fig. 1. Text-fig. 2 was constructed by counting the number of specimens in two overlapping 1-mm grid systems and taking the means of the overlapping quarters, thus tending to diminish the difference between the groups. The trend of *M. coranguinum*, with its periproct situated at about two-thirds of the total height, is clearly seen. *M. gibbus* has a less well-defined trend showing a much lower periproct. The fact that regions of low concentration of specimens occur between the two groups is significant in view of the fact that Kermack (1954) showed Rowe's collection to be biased in favour of intermediary forms.

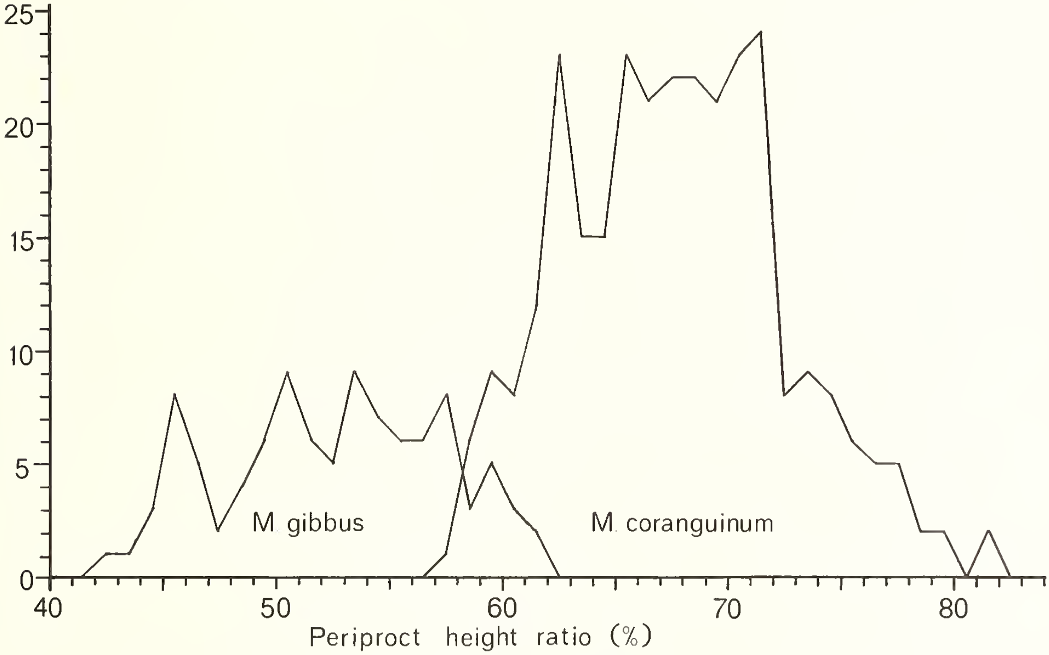


TEXT-FIG. 2. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent. Density contour graph of specimens in text-fig. 1 indicating the mean number of specimens of two overlapping 1-mm grid systems plotted per 0·5 mm square. *M. gibbus* lies in the discontinuous dense areas of low periproct height. *M. coranguinum* occupies the dense area indicating a periproct height ratio of about two-thirds.

A frequency distribution of the periproct height ratios does not reveal any bimodality unless, as in the hypothetical example given by George (1971, fig. 17), the sample is first subjectively or arbitrarily divided and the two species plotted independently, thus avoiding the frequencies of a particular ratio common to both species being compounded. Text-fig. 3 shows such a frequency distribution in which the sample was arbitrarily divided along the dotted line in text-fig. 1. The latter passes through the areas of low concentration in text-fig. 2. The calculated regression lines of the two species drawn on text-fig. 1 result from this division.

The lack of bimodality in text-fig. 3 is most probably due to a combination of several factors, two of which were discussed by Kermack (1954). Firstly, Rowe's sample of his '*Epiaster*' *gibbus* is too small for any bimodality to make itself apparent, and, secondly, the ratio of two variates is not a constant but is almost always allometric. The fact that the sample is biased in favour of intermediate forms, as well as *M. gibbus*, increases the difficulty in obtaining bimodality.

Like Kermack, I regard *M. gibbus* and *M. coranguinum* as distinct species between which intermediates occur presumably as a result of interbreeding.

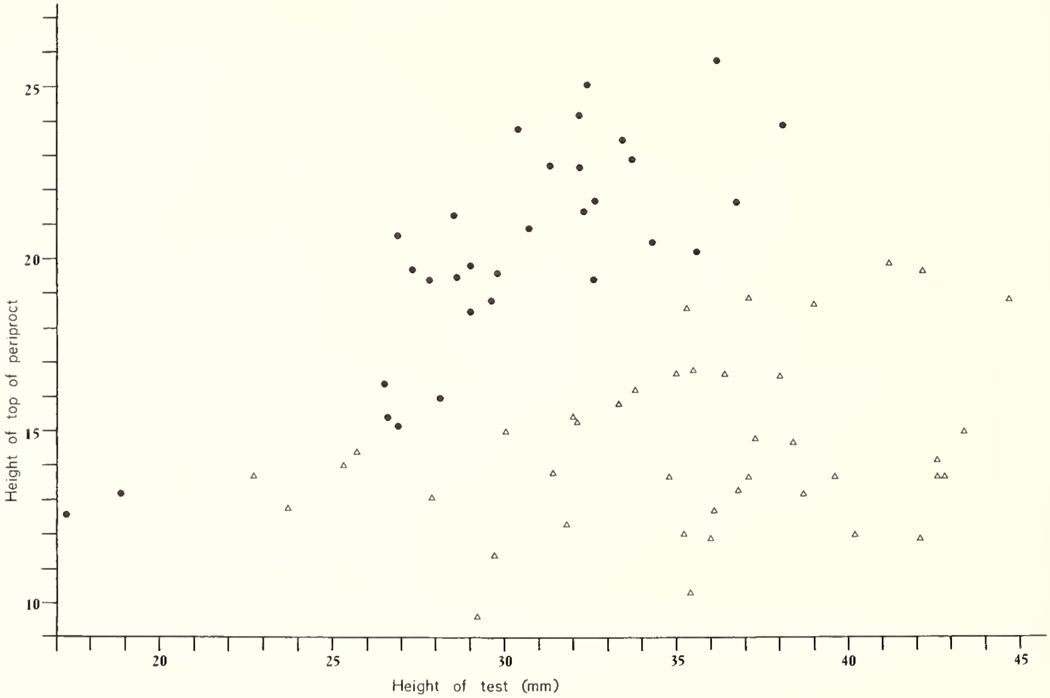


TEXT-FIG. 3. Rowe's collection of *Micraster* from the *coranguinum* Zone of Northfleet, Kent. Frequency distribution of the periproct height ratio. The sample was divided along the dotted line shown in text-fig. 1 which passes through the low density areas of text-fig. 2. Vertical axis indicates number of individuals.

M. STOLLEYI AND THE *M. SCHROEDERI–GLYPHUS* LINEAGE FROM THE UPPER CAMPANIAN OF NORFOLK

Material. Seventy-two specimens from the *mucronata* Zone of Norfolk in the collections of the British Museum (Natural History) (Rowe Collection), Institute of Geological Sciences (H. B. Woodward Collection), and the Norwich Castle Museum (Rose and Brydone Collections). Where information on museum specimens allowed, they were assigned to more narrowly defined horizons within the *mucronata* Zone from information given in Peake and Hancock (1961, 1970). The *mucronata* Zone succession is: Basal, Eaton, Weybourne, Beeston, and Paramoudra Chalks, the Weybourne and Beeston Chalks being separated by the Catton Sponge Bed. *M. stolleyi* is represented by 1 specimen from Tharston (Basal Chalk), 6 from Weybourne and Weybourne-Old Hythe, and 4 from Harford (Weybourne Chalk), 5 from Catton (Catton Sponge Bed), 1 from Whitlingham, 1 from Overstrand, 6 from Thorpe (Paramoudra Chalk), and 17 others for which the locality is unknown or vague (e.g. 'Norwich'). The *M. schroederi–glyphus* lineage is represented by 1 specimen from Stonehills (Eaton Chalk), 3 from Weybourne and Weybourne–Old Hythe, and 9 from Harford and Harford Bridges (Weybourne Chalk), 2 from Catton (Catton Sponge Bed), 4 from Whitlingham (Paramoudra Chalk), and 12 others with unknown or vague localities.

Results and conclusions. In order to obtain samples of statistically valid size, both Kermack (1954) and Nichols (1959) were forced to treat all the *mucronata* Zone *Micraster* as though they came from one horizon. Text-figs. 4 and 5*a* show that in so doing no distinct break appears between the two lineages in this zone. Text-fig. 5*b–d* is based on specimens which were assigned to more limited horizons, but statistical validity is here sacrificed.



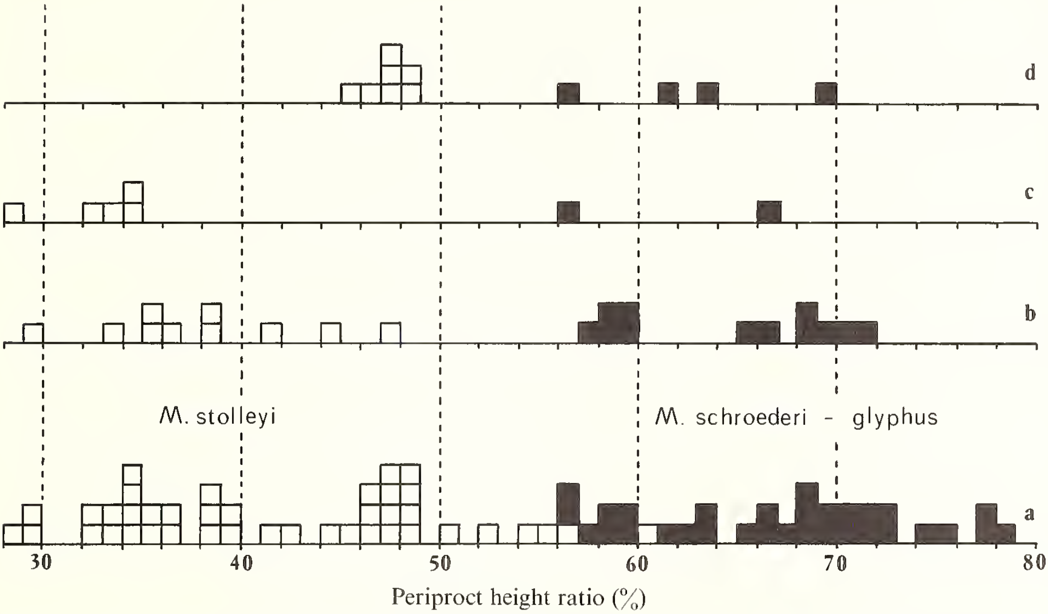
TEXT-FIG. 4. *Micraster* from the *mucronata* Zone of Norfolk. All specimens measured. Black circles = the *M. schroederi–glyphus* lineage; open triangles = *M. stolleyi*. The height of the top of the periproct is in millimetres.

The overlap of *M. stolleyi* and the *M. schroederi–glyphus* lineage in text-fig. 5*a* is almost certainly due to the effects of allometric growth on the periproct height ratio. The four specimens of *M. stolleyi* with periproct height ratios between 54% and 61% are all small (presumably juvenile specimens) ranging from 32 to 39 mm in length and from 22 to 26 mm in total height (i.e. the four specimens of *M. stolleyi* the furthest to the left in text-fig. 4). Their high periproct height ratios are a reflection of the more tumid shape typical of juvenile specimens of *Micraster*.

The periproct height ratio of the gibbous species is very variable in the *mucronata* Zone as a whole and in the Weybourne Chalk (text-fig. 5*a* and *b*), but of very limited variability at certain horizons such that it could be used to define the horizons at

Catton (Catton Sponge Bed, text-fig. 5*c*) and Thorpe (Paramoudra Chalk, text-fig. 5*d*). These changes in periproct height ratio may be a reflection of ecological conditions.

Kermack (1954) stated that there are no transitional forms between *M. stolleyi* and *M. glyphus* in the *mucronata* Zone of Norfolk where some aberrant forms, resembling in some ways *M. coranguinum*, are also found. These latter forms are most probably *M. schroederi* Stolley which is the narrow form of *M. glyphus* or, possibly, true aberrant *M. coranguinum*, which occurs in the Santonian of Norfolk, of which the horizon has been mistaken due to insufficient information on the museum specimens. Nichols (1959) concluded that intermediates exist and that they had a shorter life-span than the extreme forms (i.e. *M. stolleyi* and *M. glyphus*) which he did not regard as good species. I agree with Kermack that *M. stolleyi* and the *M. schroederi–glyphus* lineage are good species. Even if the four small specimens of *M. stolleyi* with relatively high periproct height ratios (discussed above) are regarded as intermediate in morphology to the *M. schroederi–glyphus* lineage, they are not necessarily the product of interbreeding and the two stocks can be interpreted as being genetically distinct.



TEXT-FIG. 5. Frequency distributions of the periproct height ratio of *Micraster* from the *mucronata* Zone of Norfolk. *a* = all specimens measured; *b* = specimens from the Weybourne Chalk (Weybourne, Weybourne–Old Hythe, Harford, and Harford Bridges); *c* = specimens from the Catton Sponge Bed (Catton); *d* = specimens from the Paramoudra Chalk (Thorpe and Whitlingham). Each square represents one specimen. Horizons represented in *b*, *c*, and *d* are included in *a*, but some other horizons are not shown separately.

NOMENCLATURE

Species of *Micraster* have long been renowned for their burdensome synonymies, but it is amongst the gibbous species in particular that nomenclature is most disputed. A lengthy discussion on the status of the subgenera of *Micraster* is avoided by suppressing them on the grounds that they have polyphyletic origins (Stokes 1975), but the nomenclature of the English gibbous species demands a brief explication in view of the names adopted here.

The type specimen of *M. gibbus* (Lamarck, 1816) was figured by Bruguières (1791, pl. 156, figs. 4–6) but the locality and horizon of this specimen, as well as its present whereabouts, remain unknown. However, as Valette (1907) remarked, it is more rational to think that it came from the Chalk of the Anglo-Paris basin rather than elsewhere. I have therefore proposed (Stokes 1975) that the name *M. gibbus* be restricted to gibbous forms from the Coniacian and Santonian of the Anglo-Paris basin, specimens of which agree reasonably with Bruguière's figures. Other authors have used *M. gibbus* in a different sense. Lambert (1895) restricted the name to a form from Nice which Sismonda (1843) called *M. cordatus* despite the fact that Sismonda regarded it as distinct from Bruguière's figures, that it was not figured and that the description could apply to a variety of gibbous forms. *Micraster* were unknown from Nice until the work of Sismonda and thus it is unlikely that Bruguière's specimen came from the Alpes Marîtimes. More recently, Ernst (1970) used the name for lower Campanian forms of northern Germany which ought to be called *M. fastigatus* Gauthier, 1887.

Having restricted the name *M. gibbus* to a form from Nice, Lambert (1895) intended that the name *M. senonensis* be given to the Coniacian and Santonian species of the Anglo-Paris basin. 'Le type de moyenne taille', represented by the *Epiaster gibbus* of Wright (1878), being the first of Lambert's four varieties, should be taken as the true *M. senonensis*, and the figures of Wright (1878, pl. 63) will then represent the type specimen. The label accompanying this specimen (British Museum (Natural History) E 1510) suggests, as does the text of Wright's monograph, that it comes from the upper Campanian of Harford Bridges, Norfolk, in which case *M. senonensis* Lambert, 1895 is a senior synonym of *M. stolleyi* Lambert, 1901. To avoid further confusion, I have suppressed the name *M. senonensis* and conserved *M. stolleyi* in its current usage (Stokes 1975).

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THE TRILOBITE GENUS *PHILLIPSINELLA* FROM THE ORDOVICIAN OF SCANDINAVIA AND GREAT BRITAIN

by D. L. BRUTON

ABSTRACT. *Phillipsinella fornebuensis* sp. nov. and *P. preclara* sp. nov. are described from the Caradoc Lower Chasmops Shale (4bα) and the Upper Chasmops Limestone ($4b\delta_{1-2}$) respectively of the Oslo Region, Norway, together with figured but unnamed specimens from equivalent horizons and older in Sweden. Material of *P. preclara* sp. nov. is also figured from the highest Pusgillian of northern England. The Norwegian material provides new information on muscle-scar patterns and exoskeletal surface sculpture. Well-defined glabellar lobes and furrows are described for the first time, there being three lobes in *P. preclara*, one lobe in *P. fornebuensis*. A new diagnosis is given for the genus which is retained in a separate family on account of the distinctive hypostoma. Relationship to the early scutelluids, especially *Raymondaspis* and *Stygina*, is considered likely. A classification based on the morphology of various known cranidia allows the recognition of two species groups, an Arenig–Ashgill group embracing forms from Balto-Scandinavia, eastern Ireland, Turkey, Kazakhstan, and Uzbekistan, and an Ashgill species group centred around *P. parabola sensu lato* known from Britain, Bohemia, Poland, and southern Sweden.

THIS work represents part of a larger project concerned with the vertical stratigraphical distribution and description of Middle Ordovician fossils from several sections in the Oslo Region, Norway. Detailed collecting has produced a wealth of material amongst which are specimens belonging to two new species of *Phillipsinella* described herein from the Caradoc Lower Chasmops Shale (4bα) and the Upper Chasmops Limestone ($4b\delta_{1-2}$) respectively. Further specimens from equivalent horizons or older are described from Sweden, none of which has been previously figured, although occurrences have been listed by Jaanusson (1960, 1963) from the Uhaku Stage (zone of *Glyptograptus teretiusculus*) of Öland and the Siljan district.

The importance of the Norwegian and Swedish material is that it is all of pre-Ashgill age and thus helps to shed some light on the origin and distribution of the genus *Phillipsinella* otherwise best known through its type species, *P. parabola* (Barrande), which is abundantly represented in rocks of Ashgill age in Bohemia, Britain (for discussion see Whittington 1950, 1966, 1968; Ingham 1966, 1970; Price 1973), eastern Ireland (Dean 1974), Poland (Kielan 1960), Kazakhstan (Appolonov 1974), and Usbekistan (Abdullaev 1972). In discussions on trilobite migration, Kielan (1960, p. 38) suggests a Scandinavian origin for *Phillipsinella*. The material described herein and that recently described by Dean (1973, p. 309) from the Arenig of Turkey, shows that the early history of the genus appears to lie within the Asaphid Province.

Family PHILLIPSINELLIDAE Whittington, 1950
Genus PHILLIPSINELLA Novák, 1885

Type species. By original designation, *Phacops parabola* Barrande, 1846, p. 6, from the Králuv Dvůr Formation (Ashgill), Bohemia.

[Palaeontology, Vol. 19, Part 4, 1976, pp. 699–718, pls. 104–108.]

Diagnosis. Cephalon as long (sag.) as wide, moderately convex; glabella clavate, defined by deep furrows, narrowest between palpebral lobes, widest across frontal lobe. Three glabellar furrows on suitably preserved material, otherwise shallow to lacking. Dorsal furrows end in anterior pit alongside frontal lobe; second (posterior pit) in furrow nearly opposite front of palpebral lobe. Facial sutures opisthoparian, anterior branch diverging forward, curving to meet along anterior margin. Connective sutures diverge inwards and backwards, rostral plate long (sag.), lying beneath frontal glabellar lobe. Hypostoma elongate (sag.) covering posterior half of glabella and slightly beyond posterior margin; middle body oval in outline, anterior wings short. Free cheek with genal spines extending the length of thorax. Thorax with six segments, pleural furrows shallow. Pygidium semicircular to quadrate in outline with small postero-median notch. Rachis long, slightly tapered, moderately convex with post-rachial ridge best seen on internal moulds; three to six rachial rings; pleurae smooth or with at least three shallow furrows. Glabella with raised line pattern with or without associated pits. On pygidium, raised lines along postero-lateral border and doublure.

Stratigraphical and geographical range. Ordovician (Arenig to Ashgill); Scandinavia, Turkey, Kazakhstan, Uzbekistan, Czechoslovakia, Poland, Britain, and eastern Ireland.

Discussion. The new diagnosis is emended from that of the Treatise (Harrington *et al. in* Moore 1959, p. O408) so as to incorporate new material together with study of topotype material of the type species from the Králuv Dvůr Shale, Czechoslovakia, and from the Upper Drummuck Group, Girvan (Begg Collection, Hunterian Museum, University of Glasgow), the Ashgill of Wales and northern England (Sedgwick Museum, Cambridge), and from northern England figured by Ingham (1970).

The large collection of *Phillipsinella preclara* sp. nov. is excellently preserved and provides much new information on morphology, but difficulties arise in comparing it with material assigned to *P. parabola* and allies which are mainly described from siltstone and shale, or as external moulds from decalcified limestone.

REMARKS ON MORPHOLOGY

Glabellar lobation. P. preclara shows for the first time details of glabellar lobes and furrows which, following Jaanusson (1956, pp. 36–37), are numbered and lettered from the posterior forwards, using the notation L (glabellar lobe) and S (glabellar furrow); (see Pl. 106, fig. 2). The lobes and furrows occur on the narrow posterior half of the glabella adjacent to the wide dorsal furrow, the lobes being accentuated on account of the granulation covering them, and which is absent from the furrows. There are no traces of furrows in front of S_3, on the large, forwardly expanded frontal glabellar lobe and which, on the ventral side, is underlain by the large rostral plate (Pl. 105, fig. 6; see also Whittington 1950, pl. 75, figs. 4, 6). The basal glabellar lobe (L_1) is the most prominent and forms a lateral expansion of the hindmost part of the glabellar immediately in front of the occipital furrow. This expansion together with S_1 is on specimens of *P. fornebuensis* (Pl. 107), on the cranidium of *Phillipsinella* sp. indet. B (Pl. 105, fig. 7), and on *P. parabola hibernica* (see Dean 1974, pl. 29, fig. 6). In these, however, unlike in *P. preclara*, additional lobes and furrows are faint or lacking. One specimen of *P. parabola*, illustrated by Kielan (1960, Pl. 5, fig. 1; lowermost), shows what may be a basal glabellar lobe, while other specimens do not, and lobes are lacking on material figured by Whittington (1966, pl. 25, figs. 1, 6) and Ingham (1970, pl. 5, figs. 13, 15, 16, 18). However, on the latter material, absence of lobes may be a result of preservation.

Median occipital tubercle. Unlike specimens of *P. parabola sensu lato*, *P. preclara* (Pl. 104, figs. 3, 5, 6; Pl. 105, fig. 8) and the cranidium of *Phillipsinella* sp. indet. B (Pl. 105, fig. 7) possess a median occipital tubercle. In *P. preclara* suitably preserved specimens show the tubercle to contain four tiny pits arranged to outline corners of a square. A similar arrangement of pits is also seen on the occipital ring of *P. fornebuensis* (Pl. 107, fig. 4), but in this species there is no occipital tubercle. Such a feature has been termed a median occipital organ by Whittington (1965, p. 297) in connection with scutelluids such as *Bronteopsis* and *Raymondaspis* and it is also known from several other trilobites, among them certain odontopleurids (Whittington 1956, p. 177; Burton 1967, p. 220).

Muscle scars. Cranidia of *P. preclara* and *P. fornebuensis* show small, slightly depressed smooth areas along the median line of the frontal glabellar lobe. These are here termed *frontal glabellar scar(s)*. In *P. preclara* (Pl. 104, fig. 5; Pl. 105, fig. 2) a single scar occurs on the frontmost part of the glabellar lobe, whereas in *P. fornebuensis* (Pl. 107, fig. 2) at least three separate oval scars occur along the median line. In both species these scars are accentuated by a disruption in the raised line pattern surrounding them and Plate 106, fig. 3 shows how, in *P. preclara*, the raised lines do not cross the scar.

On the pygidium of *P. preclara* (Pl. 106, fig. 1) there are smooth areas at the inner ends of each rachial ring furrow and adjacent to the dorsal furrow: these are interpreted as areas of muscle attachment. This is supported by a pygidium of *Phillipsinella* sp. indet. (Pl. 108, fig. 12), from the Lower Jonstorp Formation, Västergötland, Sweden, where similar muscle scars correspond to raised areas on the internal mould. This pygidium also has a drawn out post-rachial ridge of the rachis, which seems to be a generic characteristic and is seen even on a dorsal exoskeleton, as a light reflective area (cf. Pl. 105, fig. 4; Pl. 108, figs. 5, 6). A similar muscle-scar pattern was figured by Whittington (1965, pl. 57, fig. 13) on the pygidium of *Raymondaspis reticulatus*.

Anterior and posterior pit. The new species of *Phillipsinella* show two prominent pits in the dorsal furrow of cranidia, termed anterior and posterior pits by Kielan (1960, p. 73). These have been identified on Ashgill material by Whittington (1966, p. 79) and Ingham (1970, p. 36) and recently by Dean (1973, p. 311) on the holotype of *P. borealis* described by Kummerow (1927, pl. 1, fig. 7) from an ?Arenig erratic boulder in East Germany.

The anterior pit, which is known on certain scutelluids such as *Stygina* (see Skjeseth 1955) and *Raymondaspis* (see Whittington 1965, pl. 55, fig. 9; pl. 59, fig. 7), occurs alongside the frontal glabellar lobe and inside where the anterior branch of the facial suture crosses the border. It is especially prominent on *P. fornebuensis* (Pl. 107, fig. 1), less so on *P. preclara* (Pl. 104, fig. 1), but in both it is associated with a slight swelling on the frontal glabellar lobe when viewed from above. On the ventral surface of the dorsal exoskeleton the anterior pit corresponds to a slight boss which protrudes ventrally and is covered by the doublure of the free cheek. There is no corresponding feature on the external surface of the doublure (Pl. 105, fig. 6).

The posterior pit occurs in the dorsal furrow level with the anterior edge of the palpebral lobe where the glabella becomes constricted. Unlike the anterior pit, which is oval, the posterior pit is narrow and slit-like. On external moulds this is difficult to see, but from its position it might lie beneath the outer tip of the anterior wing of the hypostoma, and be some form of attachment point. The reconstruction given for the ventral side of the cephalon by Kielan (1960, p. 74, fig. 19) is quite misleading. Furthermore she states (p. 73) that 'p 1' (anterior pit) is situated at the level of the most anterior portion of the eye (whereas on her text-fig. 18 it is shown in front of the eye), and 'p 2' (posterior pit) is a little in front of 'p 1' (in fact it is behind 'p 1'). As far as can be judged, however, the position of the pits shown on her figure (loc. cit., fig. 18) corresponds to that observed for *P. preclara*, *P. fornebuensis*, and others.

External exoskeletal surface. P. preclara and *P. fornebuensis* have been collected from fresh, dark-grey limestone and have needed little preparation except for removal of matrix from furrows and adjacent to suture lines. The illustrated material shows details of exoskeletal sculpture of pits, granulation, and raised lines, or a combination of all three types, which are now described for *P. preclara*.

Pits. A dense irregular network of pitting without associated raised lines occurs on the anterior border of cranidia and is concentrated around the base of the frontal glabellar lobe (Pl. 105, fig. 2). Laterally, the concentration diminishes and adjacent to the anterior facial suture the border is smooth (Pl. 104, fig. 5). On the outer part of the palpebral lobe a larger, more regular pitting occurs in a series of subparallel lines, while the remainder of the lobe is smooth. A similar irregular network of pits to that on the anterior border occurs between the raised lines on the frontal glabellar lobe and on the median and posterior portion of the glabella where raised lines are lacking. Pits also occur on the free check but are lacking on the pygidium.

Granulation. On two cranidia (Pl. 104, figs. 1–3; Pl. 106, fig. 2) a dense granulation covers the entire fixed cheek, posterior border, and occipital ring but is less obvious on the holotype (Pl. 104, figs. 4, 5) and a second specimen (Pl. 104, fig. 6) where the concentration is less. On all specimens there is granulation on the glabellar lobes (Pl. 106, fig. 2), the basal part of the glabella immediately in front of the occipital furrow, and in the spaces between the pits on the posterior part of the glabella, where rows of granules also occur on the tops of many of the raised lines (Pl. 104, fig. 6; Pl. 105, fig. 2); sometimes rows of granules merge to form raised lines (Pl. 106, fig. 2).

On the pygidium granulation occurs on the pleural areas, the posterior half of the articulating half-ring, the first rachial ring, and the median portion of the remaining rachis. The distribution of granules around the smooth muscle-scar areas serves to outline the latter.

Raised lines. These occur in more or less concentric rows on the frontal glabellar lobe and outline the latter. The outermost lines start low down on the frontal glabellar lobe where they are inclined upwards and slightly outwards (Pl. 104, fig. 4). From here towards the median line, successive lines become less inclined, lower in profile, and are progressively lengthened backwards, the penultimate line always extending backwards to reach the back of the glabella. Considerable variation in the arrangement of the raised line pattern is exemplified by the illustrated specimens, for example, the three innermost raised lines on the cranidium illustrated on Plate 104, fig. 3, all reach the back of the glabella. On the largest specimen (Pl. 104, fig. 6), the outermost raised lines all curve parallel to the anterior margin, whereas those inside become straighter and extend more or less transversely across the glabella. Not all lines are continuous, those antero-medially terminating at the edge of the smooth frontal glabellar scar (Pl. 106, fig. 3) and not crossing it, while spaces between adjacent lines are occasionally taken up by short discontinuous lines with or without associated granules (Pl. 106, figs. 3, 4). Stereoscan photographs of the surface of the holotype show the raised lines to be symmetrical in section with rounded tops; they do not appear to be of the same terrace-line type described for illaenids by Whittington (1965, p. 386) in which the pattern is the result of a steep scarp and shallow-angled dip-slope topography of the exoskeletal surface.

On the pygidium, raised lines with or without granules along their length, are restricted to the articulating facet and the outer, antero-lateral part of the pleurae. The lines run subparallel to the angle of the articulating facet, and, on reaching the margin, curve sharply backwards and downwards and continue along the ventral edge of the doublure.

EXPLANATION OF PLATES

Except where stated, dorsal, lateral, and anterior views of cranidia have the specimen oriented so that the plane passing through the posterior margin of the occipital ring is vertical. All specimens painted with dilute 'Opaque' and coated with ammonium chloride.

EXPLANATION OF PLATE 104

Phillipsinella preclara sp. nov. from Upper Chasmops Limestone (4bδ_2), 1·5–1·6 m below Tretaspis Shale, Frognöya, north-west shore, Ringerike, Norway (except fig. 6).

Figs. 1, 2. PMO 94287. Cranidium, dorsal and oblique left lateral view, × 16. Coll. Bruton and Hamar.

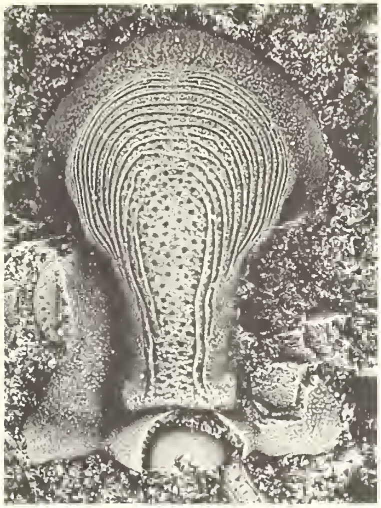
Fig. 3. PMO 8980. Cranidium, dorsal view, × 20. Loose block. Coll. J. Kiær.

Figs. 4, 5. Holotype, PMO 94278. Cranidium, left lateral and dorsal view, × 18.

Fig. 6. PMO 94288. Cranidium, dorsal view, × 16. Upper Chasmops Limestone (4bδ_1), approximately 2 m from top, Terneholmen, Asker, Oslofjord. Coll. J. Kiær.

Fig. 7. PMO 94286. Pygidium, dorsal view, × 16.

Fig. 8. PMO 9107. Free cheek, latex cast of external mould, dorsal view, × 15.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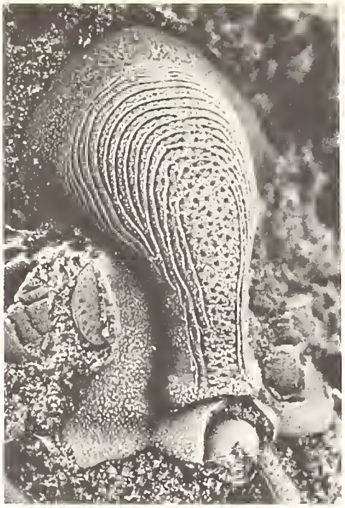
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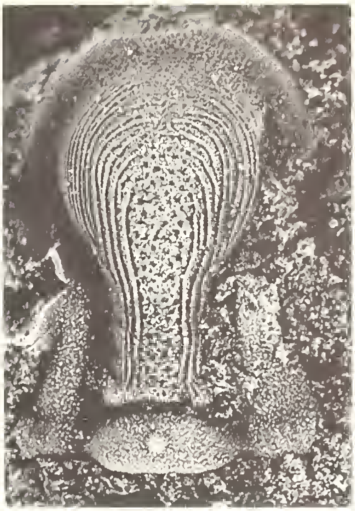
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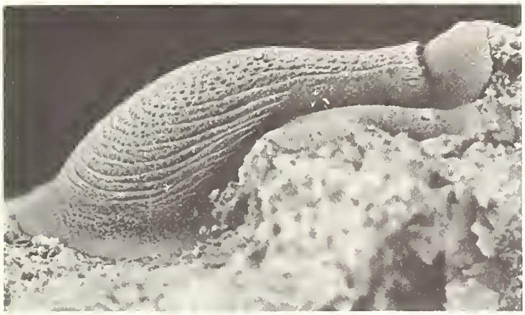
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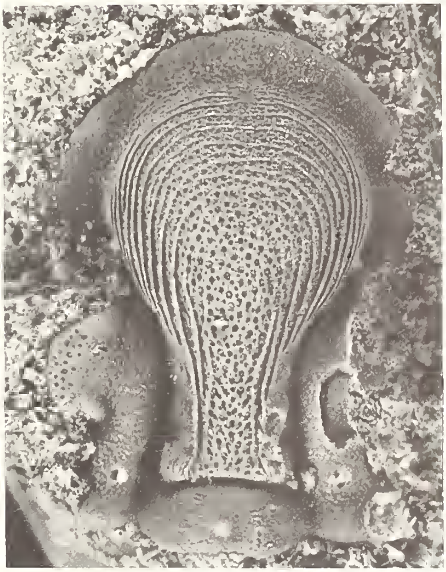
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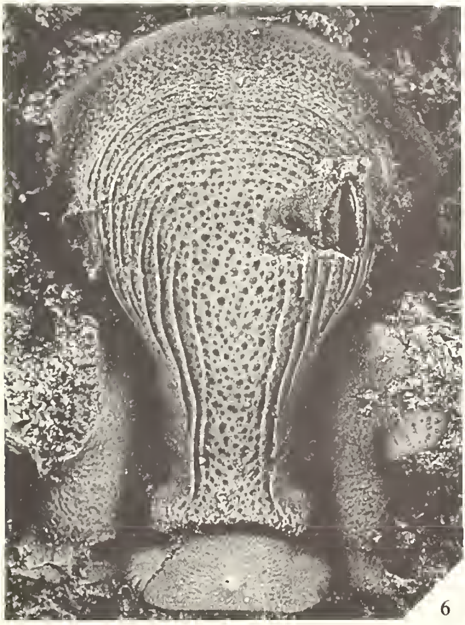
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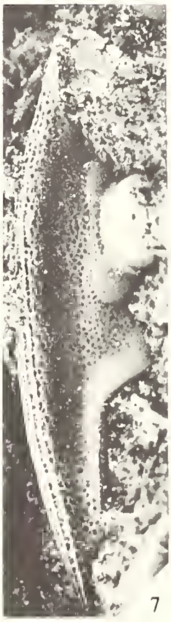
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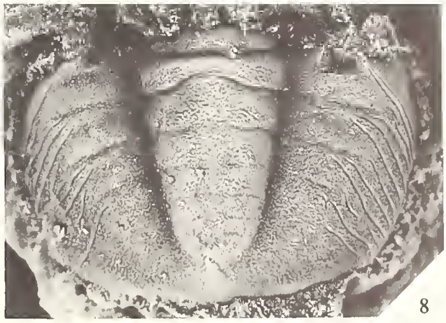
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BRUTON, *Phillipsinella*

AFFINITIES AND RELATIONSHIPS

Phillipsinella can be compared with early scutelluid genera (Whittington 1963, p. 83), particularly *Stygina* and *Raymondaspis*. Points of cephalic similarity are: three pairs of glabellar furrows, forwardly expanding glabella, course of anterior branch of facial suture, and presence of anterior pit. These dorsal features, together with the presence of a frontal glabellar scar, median occipital organ, post rachial ridge of the pygidium, and the arrangement of muscle scars, suggests that *Phillipsinella* is more closely related to *Raymondaspis* (cf. *R. reticulatus* Whittington, 1965, pl. 55, fig. 9; pl. 56, figs. 1–10; pl. 57) than to *Stygina*. Poulsen (1969, p. 409) has shown how cranidia and pygidia of *Stygina* can be separated from those of *Raymondaspis*. There is considerable difficulty in distinguishing external moulds of small pygidia of *S. minor* (see Skjeseth 1955, pl. 3, figs. 4, 6) from those of *P. preclara* occurring in the same beds. The similarity between *Phillipsinella* and *Stygina* was mentioned by Reed (1931, pp. 11–12), but was dismissed by Whittington (1950, p. 561), mainly on account of the distinctive hypostoma and rostral plate in *Phillipsinella*. More recent descriptions of the hypostoma of *Phillipsinella* by Kielan (1960) and Ingham (1970), and based on better material than was available at the time to Whittington, shows the presence of anterior wings and a more oval outline, but even this material shows that the hypostoma is unlike that known for the scutelluids including that of *R. reticulatus* (cf. Whittington 1965, pl. 55, figs. 2, 3, 5–8).

The distinctiveness of the hypostoma of *Phillipsinella* leads me to retain the genus in a separate family, the Phillipsinellidae, although the genus was probably derived from the same root stock which gave rise to the early scutelluids. Text-fig. 1 illustrates the relationship between species of *Phillipsinella* from the Arenig (Dean 1973) to Ashgill. Lack of clear-cut differences between the various pygidia which have been figured indicates that it is very difficult to separate them. Study of well-preserved *P. preclara* shows that smaller specimens have a more steeply sloping pleural margin than do larger specimens, and the indented posterior margin is more accentuated. Variation

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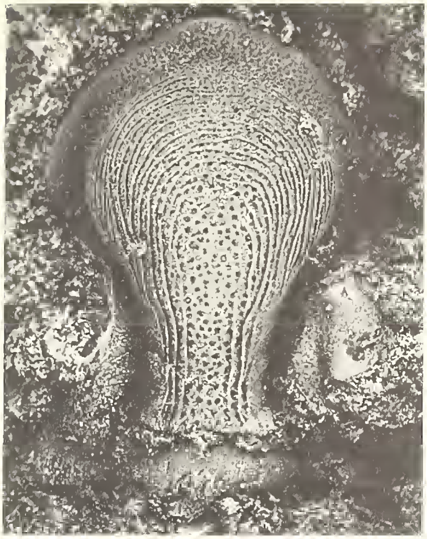
EXPLANATION OF PLATE 105

Figs. 1–3, 4, 8. *Phillipsinella preclara* sp. nov. 1, PMO 8979. Cranidium, dorsal view, ×16. Loose block, same locality and collection as Pl. 104, fig. 3. 2, segment of frontal glabellar lobe of holotype showing details of surface sculpture, ×56 approx. 3, PMO 94276. Cranidium, dorsal view, ×16. Upper Chasmops Limestone ($4b\delta_2$), Frognöya, Ringerike, Norway. Coll. Henningsmoen and Nikolaisen. 4, PMO 94284. Pygidium, dorsal view, ×22. Same locality and collection as Plate 104, fig. 1. 8, detail of occipital ring of holotype showing median occipital organ. The centre mark is a blemish on the specimen and not a pit, ×56, approx.

Fig. 5. *Phillipsinella* cf. *parabola* (Barrande 1846). RM Ar. 9880. Incomplete cephalon, dorsal view, ×3·5. Upper Jonstorp Formation (= Red Tretaspis Mudstone), Kungslena, Västergötland, Sweden.

Figs. 6, 9. *Phillipsinella preclara* sp. nov. 6, HM A7331/1. Rubber cast from external mould of enrolled specimen, ventral view showing rostral plate, connective sutures, and form of enrolment, ×4. 9, HM A7331/2. Rubber cast from external mould of incomplete cephalon, dorsal view, ×6. Highest Pusgillian Stage, Billy's Beck, Cross Fell Inlier, Cumbria, England.

Fig. 7. *Phillipsinella* sp. indet. B. LO 1941t. Cranidium, dorsal view, ×6. Tretaspis Shale, Röstånga, Kyrkabäck, Scania, Sweden. Specimen the original of Olin 1906, pl. 2, fig. 18.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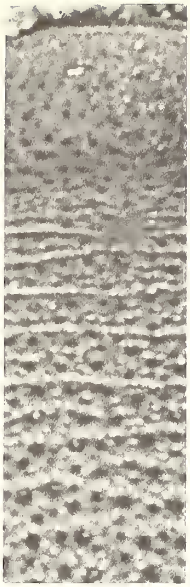
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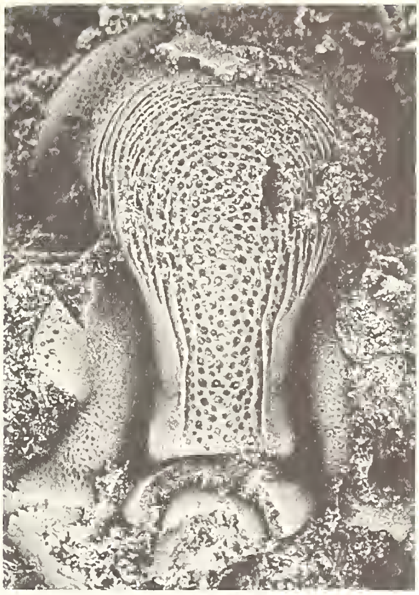
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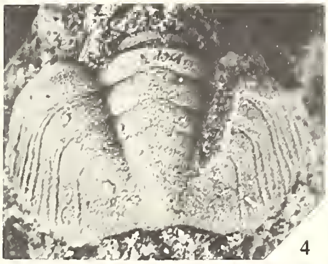
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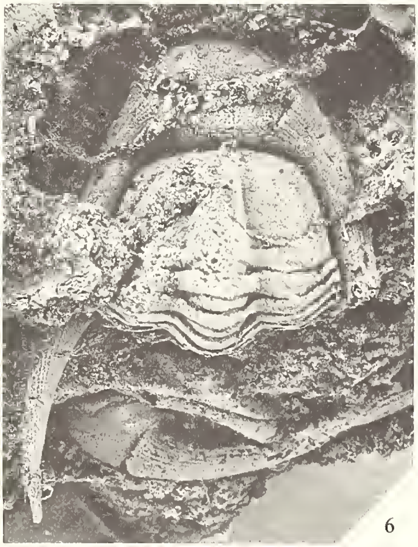
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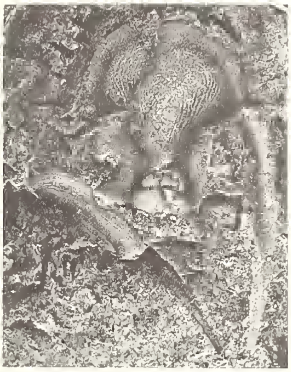
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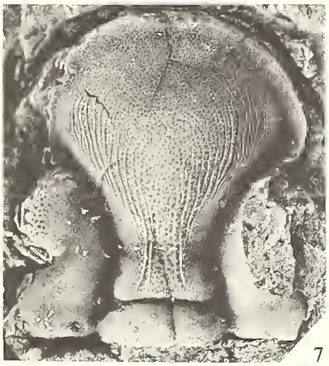
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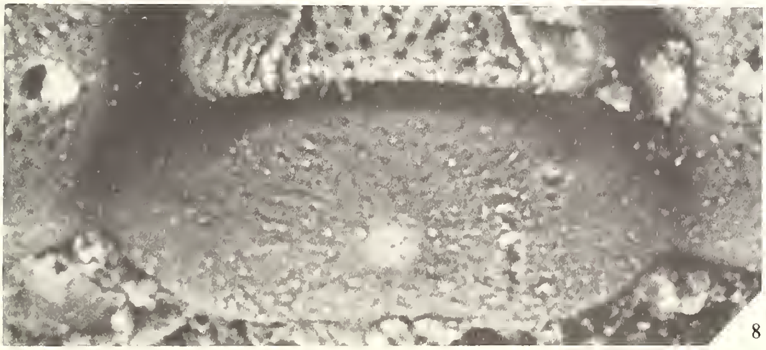
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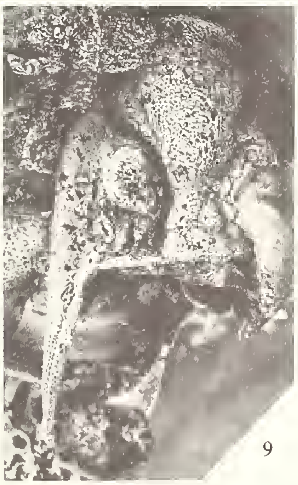
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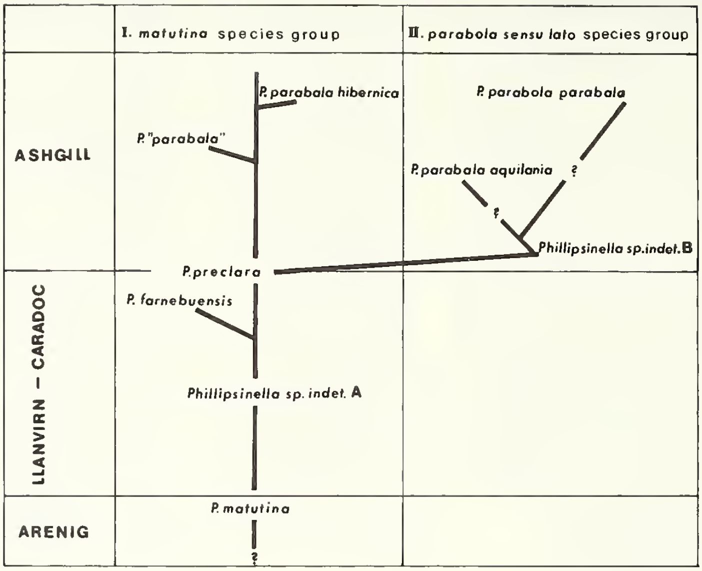
BRUTON, *Phillipsinella*



TEXT-FIG. 1. Stratigraphical distribution of *Phillipsinella* and relationship between the *matutina* species group and the *parabola sensu lato* species group. I. *matutina* species group: *P. matutina* Dean, Upper Arenig (Volkhov Stage), Turkey. *Phillipsinella* sp. indet. A. Llandeilo (Uhaku Stage), Öland and Siljan district, Sweden. *P. fornebuensis* sp. nov., Caradoc. Lower Chasmops Shale (4bα), Oslo Region, Norway; Skagen Limestone, Siljan district, Sweden. *P. preclara* sp. nov. Caradoc–low Ashgill. Upper Chasmops Limestone ($4b\delta_{1-2}$), Oslo Region, Norway; high Pusgillian, Cumbria, England. *P. parabola hibernica* Dean. Ashgill, Chair of Kildare Limestone, eastern Ireland. *P.* '*parabola*'. Ashgill, zone of *Staurocephalus clavifrons*, Kazakhstan (see Appolonov 1974) and Bukantau, Uzbekistan (see Abdullaev 1972). II. *parabola sensu lato* species group: *Phillipsinella* sp. indet. B. Tretaspis Shale, Scania, Sweden. *P. parabola aquilonia* Ingham. Ashgill. Cautleyan Stage, Cumbria, England, Upper Drummuck Group, Girvan, Scotland, Rhiwlas Limestone and Crugan Mudstones, North Wales. *P. p. parabola* (Barrande). Ashgill, Králuv Dvůr Shale, Bohemia; zone of *S. clavifrons*, Poland; Jonstorp Formation, Västergötland, Sweden.

in the number of rachial rings is also considerable, and in many cases their recognition depends on suitability of preservation of the dorsal exoskeleton, or if only internal moulds are available for study. Dean (1974, pp. 69–71) has used rachial ring count in order to distinguish the subspecies *P. parabola hibernica* Dean from the Kildare Limestone of eastern Ireland, and his specimens show four well-defined rachial rings on the dorsal surface and two to three more rings on the internal mould (see Dean 1974, pl. 29, figs. 8, 9, 12). However, rachial ring count is not a reliable taxonomic criteria because on all pygidia of *P. preclara* the first three rachial rings are clearly defined, but behind them the number of rings varies, there being three additional rings on the specimen illustrated on Plate 104, fig. 7, two rings on the specimen illustrated on Plate 105, fig. 4, and one ring on the specimen illustrated on Plate 108, fig. 9. The additional two muscle scars on the terminal portion of the rachis of the latter specimen, may also be interpreted as the sites of rachial segmentation, thus giving a total of six segments on this rachis. Similar features are more clearly shown on the internal mould of the specimen of *Phillipsinella* sp. illustrated on Plate 108, fig. 12, where a total of six segments and a terminal portion with post-axial ridge can be distinguished.

Study of cranidia shows that two morphological groups can be recognized, the Arenig-Ashgill *matutina* species group and the Ashgill *parabola sensu lato* species group.

The matutina species group. This group includes *P. matutina* (see Dean 1973, p. 309, pl. 5, figs. 2–5, 9–11) from the Arenig of Turkey, *P. borealis* Kummerow, from an ?Arenig erratic boulder (for discussion see Dean 1973, p. 311), *Phillipsinella* sp. indet. A (Pl. 108, fig. 11) from the Uhakuan of Öland, Sweden, *P. preclara* sp. nov. from the Upper Chasmops Limestone ($4b\delta_{1-2}$) of the Oslo Region, Norway, and from the highest Pusgillian Stage, Cross Fell Inlier, Cumbria, England, *P. fornebuensis* sp. nov. from the Lower Chasmops Shale ($4b\alpha$) of the Oslo Region, *P. parabola hibernica* (see Dean 1974, p. 69, pl. 29, figs. 1, 4, 6–15; pl. 30, figs. 1–3) from the Chair of Kildare Limestone, eastern Ireland, specimens from the Ashgill of Kazakhstan assigned to *P. parabola* by Appolonov (1974, p. 44, pl. 9), and specimens from the Ashgill of Bukantau, Uzbekistan, assigned to *P. parabola* by Abdullaev (1972, p. 113, pl. 45, figs. 4–9). In all but *P. fornebuensis*, cranidia are characterized by having a relatively long glabella (sag.) which is pinched in opposite the anterior edge of the palpebral lobe, the frontal glabellar lobe is smoothly rounded, and the posterior part of the glabella is relatively long (sag.) and parallel sided. The line of the anterior border follows the rounded profile of the frontal glabellar lobe and is narrowest (sag.) in the oldest species. Details of glabellar lobes are not known for the oldest cranidia, though in *P. matutina*, Dean (1973, p. 309) notes that the hindmost portion of the glabella expands slightly in front of the occipital furrow. This is best seen in the lateral view (Dean 1973, pl. 5, fig. 3) and could represent a basal glabellar lobe of the type shown in *P. fornebuensis* (Pl. 107, figs. 1, 3–7) and further well developed together with additional lobes and furrows in *P. preclara* (Pl. 104, figs. 1–6; Pl. 106, fig. 2). The cranidia of *P. parabola hibernica* (Dean 1974, pl. 29, fig. 6) also shows a basal glabellar lobe and faint traces of additional lobes.

The coarse raised line pattern with accompanying pits known from *P. matutina* is shared by the cranidium from the Uhakuan of Öland, Sweden (Pl. 108, fig. 11), and by *P. preclara* and *P. parabola hibernica* suggesting a direct relationship between them. Cranidia of *P. fornebuensis* from the Lower Chasmops Shale ($4b\alpha$) of the Oslo Region and the cranidium of *P.* cf. *fornebuensis* from the Skagen Limestone, Sweden (Pl. 108, fig. 13), on the other hand, have a finer raised line pattern without pits. The latter cranidium is too incomplete for detailed comparison but shows the broad (tr.) frontal glabellar lobe and straighter dorsal furrows characteristic for *P. fornebuensis*. The latter is considered to represent a short-lived stock confined to the Baltic and Scandinavia.

P. preclara from the Upper Chasmops Limestone in Norway is considered to be the same as specimens from the highest Pusgillian of northern England (Pl. 105, figs. 6, 9) indicating a migration into Britain of the *matutina* species group of Balto-Scandinavian origin. Whether a species like *P. preclara* gave rise to succeeding Ashgill members of the *parabola sensu lato* group in Wales, Scotland, and northern England is not known but it seems possible (text-fig. 1).

Material assigned to *P. parabola* by Appolonov (1974, p. 44, pl. 9) and by Abdullaev (1972, pl. 45, figs. 4–9), from the Ashgill of Kazakhstan and Bukantau, Uzbekistan respectively, clearly belongs to the *matutina* species group on account of glabella shape and narrow anterior border. The cranidia from both collections are most like those of *P. preclara* and *P. parabola hibernica*, but differ from these in having smaller palpebral lobes. The pointed outline of the anterior border of cranidia figured by Apollonov (1974, pl. 9, figs. 1, 2, 5, 6) is also seen in certain specimens of *P. preclara* (cf. Pl. 104, fig. 1; Pl. 105, fig. 1).

The parabola sensu lato *species group*. This group includes specimens figured from the Middle Ashgill of Poland by Kielan (1960, pl. 4, figs. 2–7; pl. 5, figs. 1–3), Scottish specimens figured by Whittington (1950, pl. 75, figs. 3–7), specimens from the Rhiwlas Limestone and Crugan Mudstones (Whittington 1966, pl. 25, figs. 1, 5, 6), material from the Cautleyan Stage (Zone 3) of northern England (see Ingham 1970, pl. 5, figs. 13, 15, 18), a cranidium of *P.* cf. *parabola* (Pl. 105, fig. 5) from the Upper Jonstorp Formation (= Red Tretaspis Mudstones), Västergötland, Sweden, and a cranidium, *Phillipsinella* sp. indet. B (Pl. 105, fig. 7) from the Tretaspis Shale of Scania. In all these specimens, even allowing for compression in some, the glabella differs from that of the *matutina* species group in being shorter (sag.), strongly pinched in at a point behind the anterior edge of the palpebral lobe, and the strongly diverging dorsal furrows produce a broader (tr.) frontal glabellar lobe. The highest part of the glabella is at a position where the glabella is pinched in, and slopes downwards and backwards from this point to the shorter (sag.), flatter posterior part of the glabella.

P. parabola aquilonia was described (Ingham 1970) as differing from *P. parabola* on account of the large flap-like palpebral lobes, and Ingham put all previously described Welsh and Scottish material in this subspecies. *P. preclara* (Pl. 104, fig. 5) also has large palpebral lobes as does the cranidium of *Phillipsinella* sp. indet. B (Pl. 105, fig. 7) from the Tretaspis Shale of Scania, Sweden, but the latter has a short

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EXPLANATION OF PLATE 106

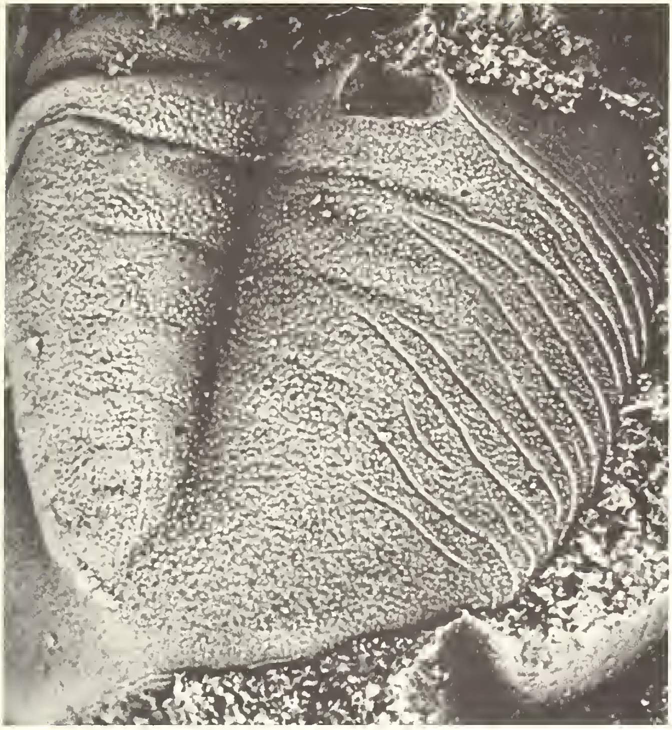
Phillipsinella preclara sp. nov.

Fig. 1. PMO 94286. Oblique view of right pleural area of pygidium illustrating rachial muscle scars and surface sculpture, ×36. Specimen the same as Plate 104, fig. 7.

Fig. 2. PMO 94287. Enlargement of glabella showing glabellar lobes (L) and furrows (S), ×40. Specimen the same as Plate 104, fig. 2.

Figs. 3, 4. Stereoscan enlargements of exoskeletal sculpture on frontal lobe of holotype. Area of enlargement shown on Plate 105, fig. 2. 3, pitted anterior border and frontal glabellar scar. Note how the raised lines do not cross this area, ×264. 4, details of raised lines lateral and posterior to frontal glabellar scar. Note that raised lines are both continuous and discontinuous and appear symmetrically rounded in profile; also pitted areas between lines, ×270. Angle of tilt, 10 degrees.

PLATE 106



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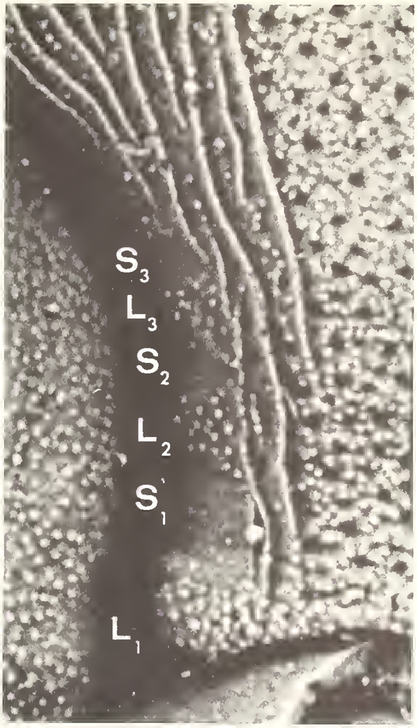

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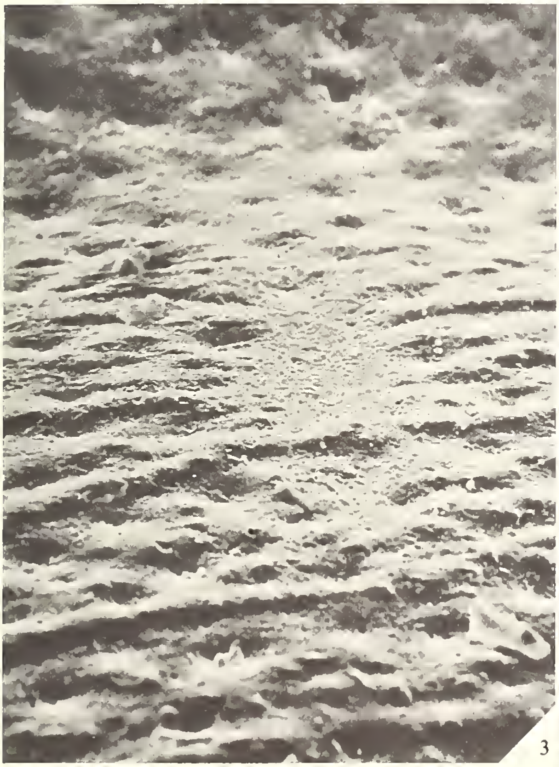

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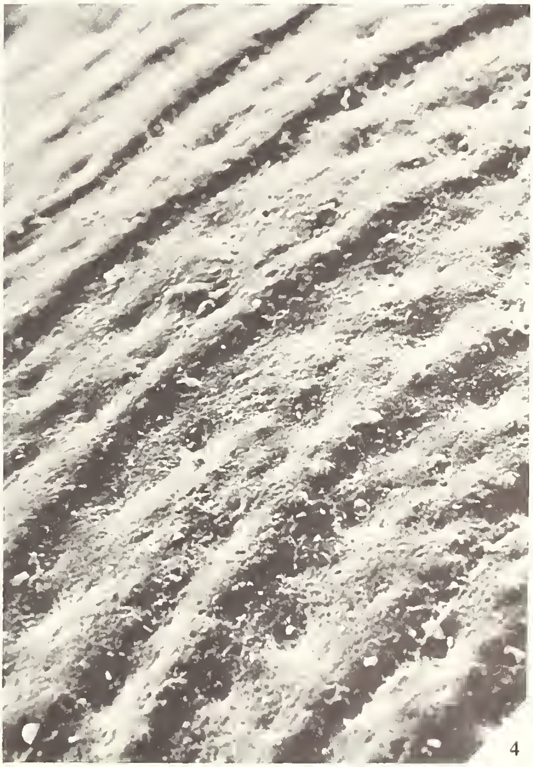

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BRUTON, *Phillipsinella*

pinched in glabella and thus resembles *P. parabola sensu lato*. However, unlike other members of the *parabola sensu lato* species group, *Phillipsinella* sp. indet. B has glabellar lobes and a median occipital tubercle known also from the Middle Ordovician *P. preclara* and *P. fornebuensis*, thus suggesting a link between the *matutina* and *parabola sensu lato* species groups.

Thus from the Arenig to Ashgill, representatives of *Phillipsinella* show variation on the same basic plan, but do not exhibit sufficient features to separate them as genera. Such variation includes size of eyes, shape of glabella (long, drawn out, short, pinched in), presence or absence of occipital tubercle, and minor differences in outline of anterior border. A combination of two or more of these characters in populations approximately the same age, but geographically separate, would indicate subspeciation. Ingham (1970) recognized this in *Phillipsinella* from the Ashgill of Britain, and it may well be true elsewhere. However, differences between specimens in pre-Ashgill rocks are more clear-cut, and the new material described below shows reliable specific differences between *P. preclara* and *P. parabola sensu lato* and between *P. fornebuensis* and the former two.

Phillipsinella preclara sp. nov.

Plate 104, figs. 1–8; Plate 105, figs. 1–3, 4, 6, 8–9; Plate 106, figs. 1–4; Plate 108, fig. 9

1953 *Phillipsinella parabola*: Störmer, p. 87.
1970 *Phillipsinella parabola aquilonia* Ingam (pars.), p. 38.

Material. Holotype: PMO 94278, a cranidium (Pl. 104, figs. 4, 5) from the Upper Chasmops Limestone ($4b\delta_2$), 1·5–1·6 m below the Tretaspis Shale, Frognöya, north-west shore, Ringerike, Norway.

Other specimens from the Upper Chasmops Limestone ($4b\delta_1$), at approximately 2 m below the top of the unit at Terneholmen, Asker, and at East Raudskjær, Asker.

As well as the holotypes and paratypes there are three cranidia and eleven pygidia.

Derivation of name. From the Latin *preclarus*—very beautiful.

Description. Cranidium with maximum width (tr.) across palpebral lobes. Glabella clavate, broadly expanded anteriorly, constricted level with anterior edge of palpebral lobe, from here backwards, parallel sided with width (tr.) in front of occipital furrow approximately half that of frontal lobe. Anterior of frontal glabellar lobe broadly rounded and separated by change in slope from flat to gently concave anterior border. Glabella with three lobes, the basal, L_1, a well-marked swelling expanding outwards and forwards towards dorsal furrow. L_2 and L_3 obliquely directed, weakly raised swellings separated by short, shallow, smooth glabellar furrows, S_1–S_3 (Pl. 106, fig. 2). Latter extend from deep dorsal furrow and are delimited at their inner ends by the raised lines on the postero-lateral side of the glabella. Dorsal furrow broad and deep opposite basal lobe, becoming shallower and directed slightly outwards and backwards to delimit occipital ring. Anteriorly, dorsal furrow becomes narrower and shallower around lateral expansion of frontal lobe and terminates in deep oval anterior pit (Pl. 104, fig. 1). A second smaller pit occurs in the dorsal furrow at a position level with the anterior edge of the palpebral lobe and where the glabella becomes constricted. Occipital ring moderately convex, longest sagitally, tapering laterally with inwardly curved posterior margin reaching ends of dorsal furrows. Occipital furrow narrow and deep medially, becoming broader and incised behind basal glabellar lobe. Small occipital node situated approximately one-third distance from posterior margin of ring. Median occipital organ with four minute pits arranged to form corners of a square (Pl. 105, fig. 8). Palpebral lobe broad and flap-like, its anterior margin level with outer end of S_1. Lobe separated from adjacent fixed cheek by shallow palpebral furrow which becomes deepened at anterior and posterior margins. In dorsal view, lobe asymmetrical with rounded posterior margin, gently curved lateral margin, and long oblique anterior margin (Pl. 104, fig. 5). Behind palpebral lobe, posterior branch of facial suture directed outwards, then curving straight backwards from shallow transverse posterior border furrow, to cross margin. Latter longest (exs.) at suture, narrowing inwards to where dorsal furrow delimits occipital ring. Inner end of anterior branch of facial suture directed outwards at about 50 degrees until a point just inside an exsagittal line through outer edge of palpebral lobe; from here, curving inwards and following curve of antero-lateral border. On all but the largest specimen (Pl. 104, fig. 6), the anterior border is slightly wider (sag.) anteriorly than laterally, thus giving the cranidium a pointed outline. On the larger specimen the curve of the anterior margin parallels that of the frontal glabellar lobe. Anterior border with thickened edge accentuated by two to three raised lines. Only one specimen of a free cheek has been found from the type locality (Pl. 104, fig. 8). The cheek is blade-like with a maximum width (tr.) across the base of the librigenal spine. Border furrow shallow anteriorly and lateral to eye lobe, deepening posteriorly and extending on to base of librigenal spine dividing latter into two parts, a raised outer edge accentuated by raised lines of the lateral border, and a narrow pitted inner edge. Lateral border flat, about half maximum width. Lateral border and furrow with fine pitted surface, bilobed base of eye socle and posterior border inside suture, smooth. A specimen (Pl. 105, fig. 6) shows details of rostral plate and connective sutures similar to *P. parabola* (Whittington 1950, pl. 75, figs. 3, 4, 6).

Pygidium. Largest pygidium (Pl. 104, fig. 7) trapezoidal with broad rachis tapering backwards and not reaching posterior margin. Dorsal furrow deepest anteriorly, shallowing backwards but outlining curved terminal portion of rachis. Latter with six ring furrows, the first crossing the rachis, curving forwards medially to form a notched posterior margin of the rachial ring. Succeeding furrows shallow and not crossing the rachis medially. Inner part of pleura flat to gently sloping outwards and crossed by three shallow pleural furrows. Latter do not reach lateral margin which slopes more steeply down and is slightly concave postero-laterally and weakly notched medially. A smaller specimen (Pl. 108, fig. 9) shows a more tapered rachis and signs on the dorsal exoskeleton of the post-rachial ridge which reaches the margin; latter indented medially. Four rachial furrows cross the rachis, and laterally there are four pleural furrows, the last one only faint. An even smaller pygidium (Pl. 105, fig. 4) shows all these features but with an additional fifth rachial ring, a more tapered rachis, very steeply sloping pleurae, and a marked posterior marginal notch.

For discussion and description of exoskeletal sculpture see p. 701.

Discussion. Material assigned by Ingham (1970, p. 38) from the high Pusgillian of Billy's Beck (Cross Fell Inlier, Cumbria), to his Cautley subspecies *P. parabola* *aquilonia*, is figured on Plate 105, figs. 6, 9, and assigned to *P. preclara*. Like the Norwegian specimens, this material has a relatively long glabella (sag.) which is pinched in opposite the anterior edge of the palpebral lobe, the frontal glabellar lobe is smoothly rounded, and the wide (sag.) anterior border likewise. Details of the glabellar lobes are not present on the Pusgillian material which consists of external moulds, but the raised line pattern and regular network of coarse pits on the glabella and anterior margin is very like that described from the better-preserved Norwegian material.

Specimens from the type horizon occur abundantly in a thick limestone bed 1·5–1·6 m below the Tretaspis Shale, together with a rich fauna including *Tretaspis kiaeri*, *Stygina minor*, *Telephina* (*Telephina*) *wegelini*, and undescribed species of *Staurocephalus*, *Sphaerexochus*, *Diacalymene*, and *Lonchodomas*. Many of these genera are also known from Pusgillian and younger strata in Britain. The significance of this fauna in terms of interregional correlation is being assessed by A. Owen (University of Glasgow), and part of the Upper Chasmops Limestone at Ringerike may be younger than previously thought (see also discussion by Dean 1971, pp. 14, 47–48).

Small cranidia of *P. preclara* from 4bδ_1 in Asker cannot be distinguished from those of similar size from 4bδ_2 in Ringerike. However, the largest cranidium known for the species is from 4bδ_1 on Terneholmen, Asker (Pl. 104, fig. 6), and it is this specimen which shows a slightly different raised line pattern and a more rounded anterior border than usual.

Phillipsinella fornebuensis sp. nov.

Plate 107, figs. 1–7; Plate 108, figs. 1–6

Material. Holotype: PMO 94297, a cranidium (Pl. 107, figs. 4, 7) from the Lower Chasmops Shale (4bα), Fornebu foreshore profile, Oslo–Asker, Norway. Other specimens from the Lower Chasmops Shale at Langmannen, Snaröya, close to the type locality, from Nakholmen, Oslofjord, and Rodelokken (Bygdöy profile 38–39 m), Oslo.

As well as the holotype and figured paratypes four cranidia and eight pygidia.

Description. The broader (tr.) glabella outlined by straighter forwardly diverging dorsal furrows in dorsal view (Pl. 107, figs. 1, 4, 5), the steeply sloping glabellar profile in lateral view (Pl. 107, figs. 6, 7), and the weaker raised line pattern and limited pitting, separates cranidia of this species from those of *P. preclara*. Other

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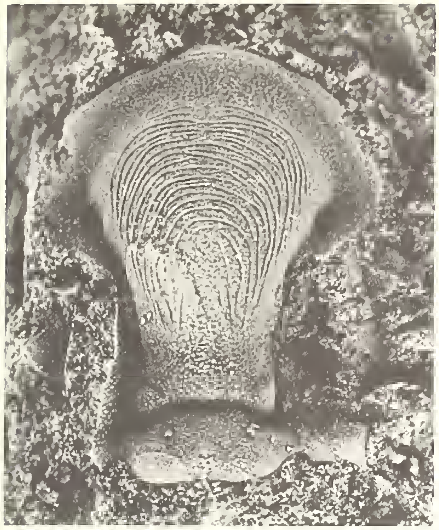
EXPLANATION OF PLATE 107

Phillipsinella fornebuensis sp. nov. All from limestone in upper part of Lower Chasmops Shale (4bα), Fornebu foreshore profile, Oslo–Asker, Norway. The height above base (normal sea level) of measured section is given in metres.

Figs. 1, 2, 6. PMO 70246: 3·20 m. 1, cranidium, dorsal view showing well-developed anterior pit, ×20. 2, anterior view showing three frontal glabellar scars and discontinuous and branching raised lines, ×36 approx. 6, right lateral view, ×20.

Figs. 3, 5. PMO 94293: 3·20 m. 3, cranidium, oblique right lateral view, ×16. 5, dorsal view, ×16.

Figs. 4, 7. Holotype, PMO 94297: 3·20 m. 4, cranidium, dorsal view, ×22. 7, right lateral view; specimen oriented with palpebral lobe horizontal, ×22. Much of the glabella has an overgrowth of secondary calcite which fortuitously gives the appearance of a partly exfoliated exoskeleton.



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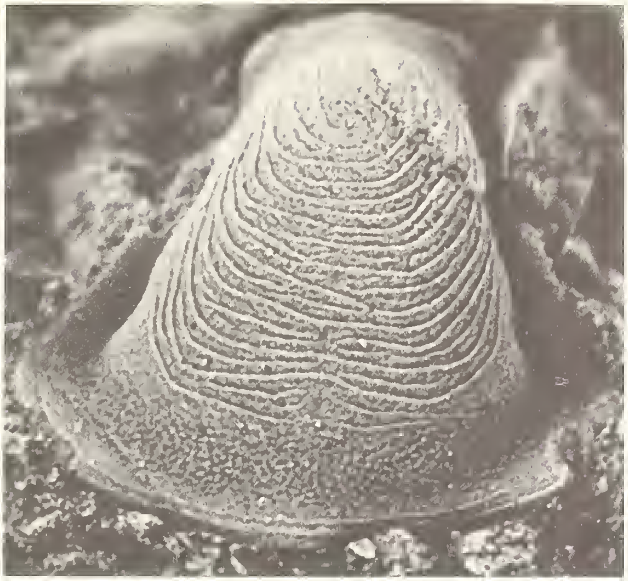

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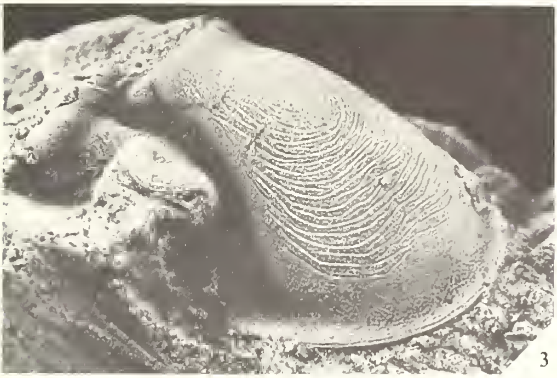

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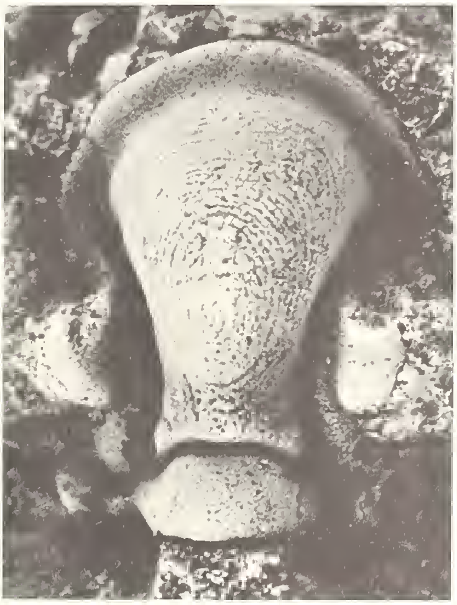

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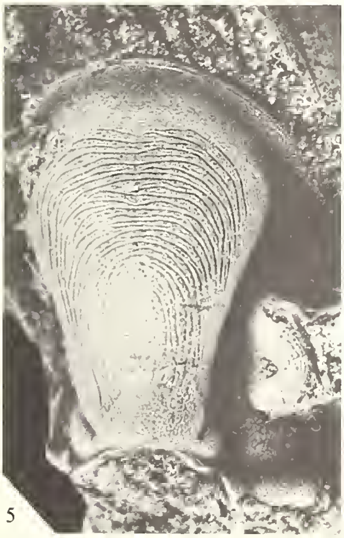

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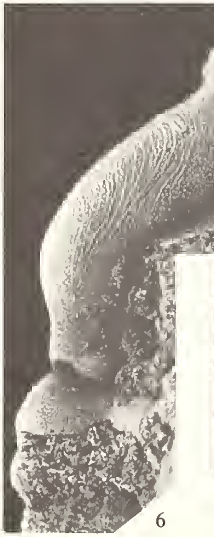

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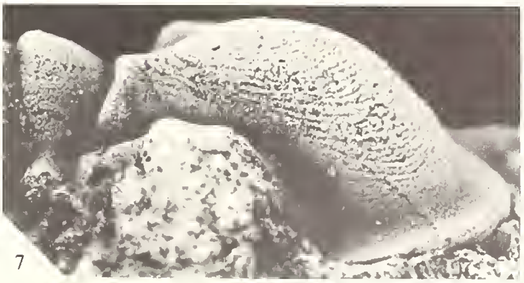

7

BRUTON, *Phillipsinella*

differences include the smaller, more rounded palpebral lobe situated on a narrower (tr.) fixed cheek (Pl. 107, fig. 5), and the broad, deep dorsal furrows. The latter end anteriorly in a conspicuously deep oval anterior pit. Only the basal glabellar lobes are developed and are outlined by the narrow, deep S_1 furrows which reach the occipital furrow. The median occipital organ, represented by four minute pits, occurs in the same position as in *P. preclara*, but an occipital tubercle is not developed (Pl. 107, figs. 1, 4). Pitting occurs only on the highest part of the glabella where it is restricted to a small oval area inside the innermost raised lines. The latter are much finer than in *P. preclara*, and on the frontal glabellar lobe are seen to anastomose (Pl. 107, fig. 2). On all specimens there are at least three smooth frontal glabellar scars (Pl. 107, fig. 2), and an interruption of the raised line pattern occurs adjacent to each scar. None of the raised lines extend as far as the back of the glabella which is covered by a dense, fine granulation. A similar granulation covers the occipital ring and anterior and posterior borders. One incomplete free cheek (Pl. 108, fig. 4) is known and this is wider (tr.) than that of *P. preclara* and lacks the pitted surface and smooth eye socle. Details of the thoracic segments are known from one partly flexed specimen showing four segments and articulated pygidium (Pl. 108, fig. 6). In shape each pleura resembles the first segment of the pygidium with short (trans.) inner portion crossed by a shallow transverse pleural furrow, and a longer outer portion which becomes bent strongly downwards and terminates bluntly. A diagonal raised line marks the shoulder of the articulating facet, and two to three shorter raised lines occur on the shoulder proper.

Pygidium. Like that described for *P. preclara*, but differing from that species in that the rachis has four rachial rings all of which cross the rachis, and there is a corresponding number of pleural furrows throughout ontogeny. Additional differences between mature *P. fornebuensis* and *P. preclara* (cf. Pl. 108, fig. 1; Pl. 104, fig. 7) are

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EXPLANATION OF PLATE 108

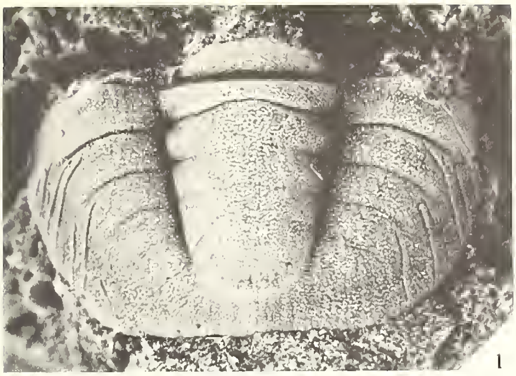
Figs. 1–6. *Phillipsinella fornebuensis* sp. nov. All from the same locality as Plate 107. 1, 2. PMO 94295: 4·80 m. 1, pygidium, dorsal view, ×10. 2, left lateral view, ×10. 3, 4. PMO 94300: 4·0 m. 3, small pygidium, dorsal view, ×30. 4, incomplete free cheek, ×25. 5, PMO 70247: 3·20 m. Pygidium, dorsal view, ×22. 6, PMO 94296: 4·80 m. Partly enrolled exoskeleton with four thoracic segments and articulated pygidium, ×21.

Fig. 9. *Phillipsinella preclara* sp. nov. PMO 94285. Pygidium, dorsal view, ×24. Upper Chasmops Limestone ($4b\delta_2$), 1·5–1·6 m below Tretaspis Shale, Frognöya, north-west shore.

Figs. 8, 13. *Phillipsinella* cf. *fornebuensis* sp. nov. 8, UMD 2000. Pygidium, internal mould, dorsal view, ×10. Skagen Limestone, 9·3–9·4 m from top of Macrourus Limestone, Fjäcka section, Siljan district, Sweden. 13, UMD 2001. Incomplete cranidium, dorsal view, ×18. Skagen Limestone, Fjäcka section, level 8·95–9·05 m.

Figs. 7, 10, 11. *Phillipsinella* sp. indet. A. 7, UMD 2002. Pygidium, dorsal view, ×22. Furudal Limestone, Profile D92, Fjäcka, Siljan district, Sweden. 10, UM Öl 1330. Pygidium, internal mould, ×18. Persnäs Limestone, Böda Hamn bore core, level 7·8 m, Öland, Sweden. 11, UM Öl 1329. Cranidium, dorsal view, ×30. Level 7·26 m, same locality and horizon as fig. 10.

Fig. 12. *Phillipsinella* sp. RM Ar. 9881. Partly exfoliated pygidium showing muscle-scar pattern on rachis and post rachial ridge, dorsal view, ×10. Lower Jonstorp Formation, Mösseberg, Västergötland, Sweden.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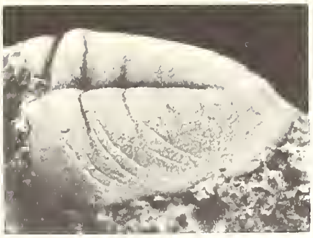
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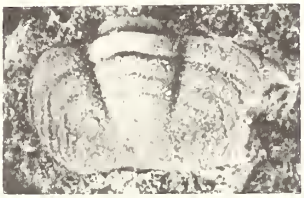
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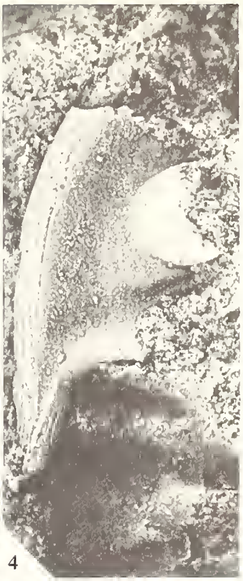
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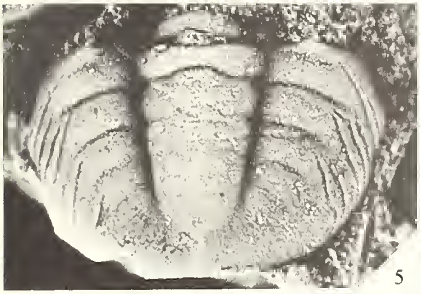
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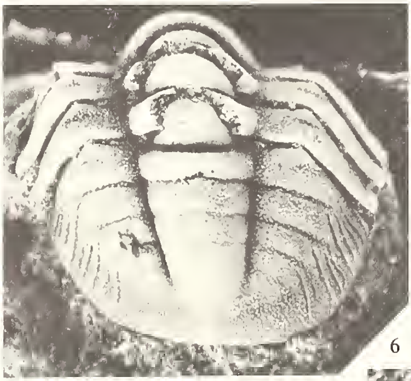
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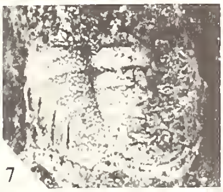
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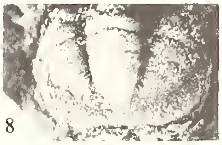
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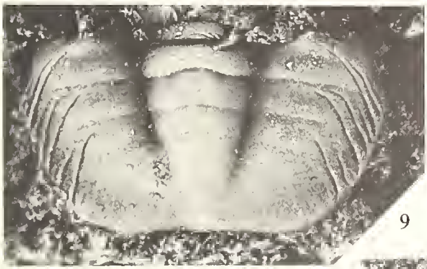
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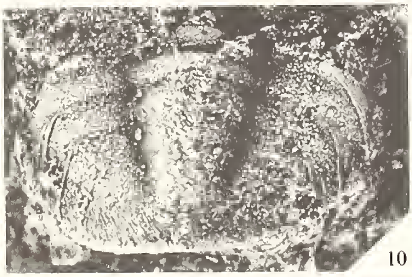
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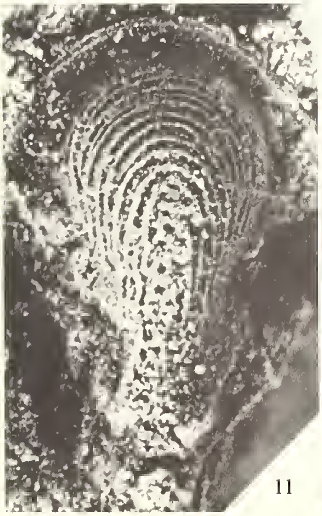
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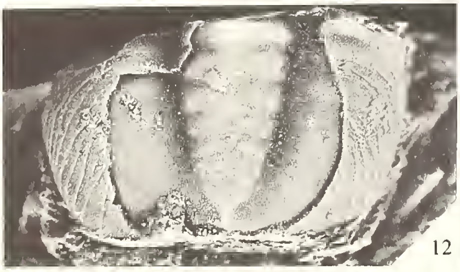
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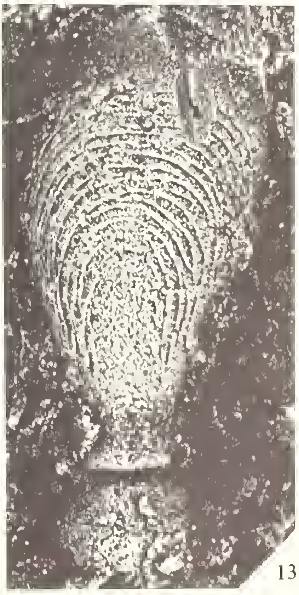
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BRUTON, *Phillipsinella*

the broader (tr.) and shorter rachis in the former and the lack of smooth muscle-scar areas. Otherwise details of exoskeletal granulation and raised line pattern are the same.

Discussion. The steeply sloping glabellar profile in lateral view, the straight, forwardly diverging dorsal furrows, and the fine raised line pattern are features shared by the incomplete cranidium (Pl. 108, fig. 13) from the Skagen Limestone of the Siljan District, Sweden (for stratigraphy see Jaanusson 1964, pp. 8, 10, 56-58), which is here referred to as *P.* cf. *fornebuensis.* A small pygidium (Pl. 108, fig. 8) from a similar horizon is also assigned here.

The type species is common in the Lower Chasmops Shale (4bα), for which it appears to be a reliable index fossil for the topmost 5 m of this unit, occurring with a rich fauna including *Platylichas validus*, *Asaphus* (*Neoasaphus*) *glabratus*, *Remopleurides* sp., *Chasmops* cf. *conicophthalmus*, and *Decoroproetus* cf. *gyratus.* All but the last-named species are listed by Jaanusson (1964, p. 56), together with *Phillipsinella* sp., as being distinctive for the Skagen Limestone in the type area of Västergötland, Sweden, indicating a correlation between this unit and the upper part of the Lower Chasmops Shale of the Oslo Region. Jaanusson (1964, p. 53) has already indicated that at least part of the Lower Chasmops Shale of the Oslo Region is also equivalent to the upper pelitic member of the underlying Dalby Formation in Västergötland on the basis of the ostracod fauna. The Dalby Formation ostracods listed by Jaanusson have not been identified in the topmost 5 m of the Lower Chasmops Shale in the Oslo Region, according to G. Qvale.

Phillipsinella sp. indet A

Plate 108, figs. 7, 10, 11

Discussion. The pygidium (Pl. 108, fig. 10) and the cranidium (Pl. 108, fig. 11) are those listed by Jaanusson (1960, p. 234; p. 236, fig. 5) from the Persnäs Limestone (Uhakuan Stage) of the Boda Hamn bore core, northern Öland, Sweden. The cranidium is incomplete, but the glabella shows the well-rounded frontal lobe and long (sag.) and narrow posterior part characteristic for the *matutina* species group. The frontal lobe slopes steeply downwards anteriorly and laterally as in *P. matutina* (see Dean 1973, pl. 5, figs. 2, 3, 9), but is longer (sag.) than in that species. The surface of the glabella is covered with a pattern of strong raised lines similar to that of *P. preclara*, and pits occur on the highest part of the glabella and on the posterior portion. The small pygidium (Pl. 108, fig. 10), an internal mould, resembles *P. preclara* (Pl. 108, fig. 9) in being more rectangular in outline than is usual for the genus, and has a straight posterior margin. The rachis has three well-defined ring furrows which laterally correspond to the same number of pleural furrows. A second pygidium (Pl. 108, fig. 7) from the Uhakuan Furudal Limestone at the main section of Fjäcka, Siljan district, Sweden, and most resembles *P. matutina* in its sub-semicircular outline. Jaanusson (1963, p. 27, fig. 10) lists a *Phillipsinella* sp. nov. from the same locality of Fjäcka at level 19·00 m in the profile. This specimen is an incomplete cranidium but shows a well rounded, narrow anterior border like that of *P. matutina* and of the specimen (Pl. 108, fig. 11) from the Uhakuan of Öland.

Phillipsinella sp. indet. B

Plate 105, fig. 7

Discussion. This cranidium was described by Olin (1906, p. 60, pl. 2, fig. 18) from the Tretaspis Shale of Scania, Sweden, but there is no evidence from his text or from the specimen label, where in the succession at Röstånga the specimen was collected, and he records *Phillipsia* [*sic*] *parabola* from various horizons (loc. cit., p. 78). Comparison between this cranidium and those of *P. parabola* from Poland (Kielan 1960, pl. 5, figs. 1, 3), shows how similar they are in glabella shape and raised line pattern, the difference between them being the larger palpebral lobe in the Swedish specimen. In glabella shape and size and position of eyes, the Olin specimen is indistinguishable from topotype material of *P. parabola* from Czechoslovakia and from the specimen (Pl. 105, fig. 5) referred to *P.* cf. *parabola* from the Upper Jonstorp Formation of Västergötland, Sweden. However, unlike these and other Ashgill members of the *parabola sensu lato* species group from Britain and Poland, the Olin specimen has glabellar lobes and furrows clearly developed, the basal lobe especially so, and the occipital ring bears a median tubercle.

Dr. J. K. Ingham has kindly shown me an incomplete internal mould of a cephalon, the only known *Phillipsinella* from the red mudstone unit of the Upper Whitehouse Beds on the foreshore south-west of Girvan, in beds containing an unusual facies fauna dominated by blind and large-eyed trilobites (Ingham pers. comm.). The cephalon is of the *parabola sensu lato* species group type and is most like topotype specimens of *P. parabola.* However, the Girvan specimen occurs below strata with *Dicellograptus complanatus* and above those with *Pleurograptus linearis* and is thus older than *Phillipsinella parabola.*

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BRACHIOPODS FROM THE HIRNANTIAN STAGE (ORDOVICIAN-SILURIAN) AT PERCÉ, QUEBEC

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ABSTRACT. The following uppermost Ordovician-basal Silurian brachiopods of Hirnantian age from the White Head Formation at Percé, Quebec, Canada, are described and illustrated: *Hirnantia sagittifera*, *Dalmanella*? sp., *Kinnella kielanae*, *Eostropheodonta siluriana*, and *Plectothyrella crassicosta*. The occurrence is the first typical North European Hirnantian brachiopod fauna from North America to be identified at the specific level.

A TYPICAL brachiopod-dominated North European Hirnantian fauna was reported from the White Head Formation at Percé, Québec by Lespérance (in St-Julien *et al.* 1972; Lespérance 1974), and this paper describes those brachiopods, supplemented by additional material collected in 1974 and 1975. As this is the first typical North European Hirnantian brachiopod fauna from North America to be identified at the specific level, the species are illustrated, briefly described, and possible clinal variation assessed.

Hirnantian brachiopod faunas have been found widely in Northern Europe and the British Isles (see summaries by Wright 1968; Lespérance 1974). A similar but specifically distinct fauna in Morocco was described by Havlíček (1971). A related fauna may also occur in the Northern Shan States, Burma (Temple 1965). In North America typical Hirnantian brachiopod genera were reported from Maine by Neuman (1968), from Gaspé, Québec (Lespérance 1974), and in Illinois and Missouri by Amsden (1971, 1974), and a trilobite-dominated fauna of probable Hirnantian age in the White Head Formation by Lespérance (1968). The brachiopod species reported from Maine were not identified in Neuman (1968), but they may be typical representatives of the fauna. The localities in Maine lie in the same depositional belt as the Percé exposures (Ayrton *et al.* 1969). Amsden (1974) reported several genera in the Edgewood Group in Illinois and Missouri and linked it to Hirnantian faunas. However, all the Edgewood species are different from those in any confirmed Hirnantian fauna. Included in this mid-continent fauna are species of the late Ordovician North American Province genera *Thaerodonta* and *Diceromyonia*, species of the Hirnantian brachiopod fauna genera *Hirnantia*, *Dalmanella*, *Cliftonia*, and *Rafinesquina* (cf. *Eostropheodonta*) [*sic*], and species of North European Province genera such as *Dolerorthis*, *Mendacella*?, *Dicoelosia*, *Coolinia*, *Eospirigerina*, and a pentamerinid (*Brevilamnulella*) which may have been derived from the North European Province but certainly not from the North American late Ordovician Province. The Edgwood fauna may be of early Silurian (post-Hirnantian) age, as correlation with the type area in the United Kingdom during this interval is very tenuous. All Hirnantian genera reported by Amsden range well into the Silurian. Thus the Edgewood fauna could be a latest Ordovician endemic North American

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fauna with species derived from the *Hirnantia* Community and other North European Province species. On the other hand, and we consider this more likely, the fauna may be a Silurian one which includes a few hold-overs from the late Ordovician North American Province. In no way can it be considered the typical brachiopod-dominated *Hirnantia* Community.

THE PERCÉ FAUNA, ITS AGE AND PALAEOECOLOGY

Lespérance (1974) reported six brachiopod species in this fauna but in fact only five are present. The brachiopods *Hirnantia sagittifera*, *Kinnella kielanae*, *Eostropheodonta siluriana*, and *Plectothyrella crassicosta* are common elements of the Hirnantian fauna. *Dalmanella*? sp. may be related to *D. testudinaria*, another typical element of the fauna. Other members of the fauna from Percé include a cornulitid (Pl. 110, fig. 6), three poorly preserved conulariids, ten small favositid colonies (with very small corallites and corallum shapes that are either cylindrical or lozenge-shaped), and a pelmatozoan. Lespérance (1968) reported six specimens of *Phillipsinella parabola* (Barrande, 1846), and a pygidium of *Mucronaspis mucronata* (Brongniart, 1822) *sensu* Temple (1952) was collected recently.

Recently our knowledge of the faunas of the Hirnantian Stage has been expanded by Cocks and Price (1975, pp. 722–723) who '. . . believe that the *Hirnantia* fauna is best interpreted as representing an animal community comparable with those described by Ziegler *et al.* (1968) . . .'. However, trilobites very often occur with brachiopods in a particular assemblage, but in others trilobites and brachiopods occur separately, a point forcibly made by Lespérance (1974). Both trilobite-dominated and brachiopod-dominated faunas were assigned to the *Hirnantia* fauna and community by Cocks and Price (1975), but we prefer to recognize separate communities and believe this conforms more closely to the community usage of Ziegler *et al.* (1968). The trilobite-dominated community is here termed the *Mucronaspis* Community, and is gradational with the *Hirnantia* Community. Gradations such as this are common in Recent level-bottom marine communities. The gradation may also vary with time, but this point needs further field work to be proven.

The *Hirnantia* Community described in this paper is a shallower-water community than the *Mucronaspis* Community (with a few graptolites and no brachiopods) which was described previously by Lespérance (1974) from the Portage River area, 17 km from Percé. The relation between these distinct communities is not inconsistent with what is known of the Scandinavian occurrences. We agree with Cocks and Price (1975) that what has previously been referred to as the *Hirnantia* fauna is best considered as a community (or communities), and we suggest that in the future the term *Hirnantia* Community be used exclusively in place of '*Hirnantia* fauna'. Application of the term Hirnantian fauna to any fauna from the Hirnantian Stage is appropriate and is not in error (as maintained by Cocks and Price 1975, p. 721). This usage is simply a reflection of the age of the fauna involved. For example, another Hirnantian fauna, not previously mentioned, is the *Holorhynchus* Community of Scandinavia (see Boucot 1975).

In the Portage River area near Percé, Lespérance (1974) reported the association of Hirnantian trilobites with a Silurian graptolite, *Climacograptus rectangularis*-

medius, indicating that the Hirnantian fauna is both uppermost Ordovician and lowermost Silurian, when correlated with the type sections in the United Kingdom. *C. rectangularis-medius* refers to specimens belonging to a single species, but for which the terms *rectangularis* and *medius* are synonyms according to Dr. J. Riva (pers. comm.). Rickards (in Cocks and Price 1975, p. 722) believes this is an Ordovician graptolite but until he gives a systematic description of the specimens in question we will follow Riva's identification and age assignment. Ingham (1974, p. 59) cited Lespérance (1974) as advocating the inclusion of the Hirnantian Stage in the Silurian. In fact Lespérance only suggested this placement as *one* of several possible alternatives, while noting (Lespérance 1974, fig. 2) that as now defined the Hirnantian Stage includes the systemic boundary. As the faunas from the mid-Ashgill to the mid-Llandovery become progressively more cosmopolitan, we now suspect that a systemic boundary drawn near the mid-Llandovery will ultimately prove to be the easiest to recognize on a world-wide scale.

It has still not been established that the top of the Hirnantian Stage corresponds with the base of the Llandovery Series. No marker point (Harland *et al.* 1972, p. 299) has been established for the standard stratigraphical scale within the Foel y Ddinas Mudstone (the type Hirnantian) of the Bala area, or for that matter in the Llandovery area. A section along forestry roads immediately north of the stream Cwm Hirnant (and immediately north of the type Hirnant Limestone quarry) has yielded a *Hirnantia* Community assemblage and is overlain (10 m above) by graptolites of the Upper Llandovery, including *Monograptus* of the *priodon* group (pers. comm., Dr. R. B. Rickards, Sept. 1974). This locality is near the locality Bwlch yr Hwch which supposedly contains *Glyptograptus persculptus*, discussed in Bassett *et al.* (1966, p. 256). As correlation between the Bala area and Dobb's Linn is at best tenuous, the type Hirnantian may consequently extend into the Llandovery, a point previously made by Lespérance (1974). This only serves to reinforce Cocks and Price's (1975) contention that occurrences of the *Hirnantia* Community (and the *Mucronaspis* Community) are probably not all of the same age.

Finally, it must be noted that should the Ellis Bay Formation faunas of Anticosti, in the North American zoogeographic province, prove to be partly of the same age as the Hirnantian Stage, the term Gamachian (Twenhofel 1928) has priority in the standard stratigraphical scale (Harland *et al.* 1972) over the term Hirnantian, which was originally suggested as a *post-Ashgill* time-stratigraphical term (Bancroft 1933).

PALAEOZOOGEOGRAPHY

The Hirnantian localities in Gaspé and Maine lie on the American margin of the Proto-Atlantic Ocean (Wilson 1966; Bird and Dewey 1970; McKerrow and Ziegler 1971, 1972). A recent review of the Taconic Orogeny in Québec (St-Julien and Hubert 1975) reveals that in the late Ordovician these areas lay oceanward (present-day east) of a tectonic welt formed during closure of a basin behind the arc. All species identified in the Percé collections are known in the North European Hirnantian Stage. The presence of this fauna on the eastern margin of North America is significant as it implies that distribution of species was possible across the closing Proto-Atlantic Ocean. The Percé fauna is more closely related to the North European Hirnantian fauna of Great Britain and Ireland than to that of Sweden or Poland. *Eostropheodonta siluriana* is known only in Great Britain and possibly Ireland. Details of the morphology of *Plectothyrella crassicosta* (described below) are most similar to the morphology of members of the species from Great Britain (indicating that clinal variation may have existed). Therefore faunal communication through Great Britain appears very likely. The Percé fauna can be distinguished from the South European–North African Hirnantian fauna by distinctive species of *Eostropheodonta* and *Plectothyrella* discussed below.

LOCALITY

The fossils were collected from a talus slope beneath the vertical cliff along the sea, north of Cap Blanc (Military Grid Reference 090729) shown on the Percé Topographic Map (22A/9 Edit. 2). The locality was discussed by Lespérance (1974). The fossils are from a 30-m band of steeply dipping red mudstones in the lower part of a 610 m continuously exposed section dominated by thinly bedded micritic limestones. To the north the mudstones are underlain by limestones with 'Lower or Middle' Ashgill faunas. To the south, at the top of the mudstones, is a minor fault above which are Llandovery limestones. In 1974 the accessible portions of the cliff outcrop were carefully examined by the authors, but no fossils could be found in place. The fossils recovered in 1974 were localized on one part of the talus slope and were probably weathered from a single bed or a closely spaced group of beds. In 1975, on the other hand, fossils were present on all portions of the talus. The fossils were clearly derived from the overlying cliffs because the lithology of the talus matches the bedrock, and the talus was actively accumulating while the collections were made.

SYSTEMATIC PALAEONTOLOGY

Family DALMANELLIDAE Schuchert, 1913
Genus DALMANELLA Hall and Clarke, 1892
Dalmanella? sp.

Plate 109, figs. 1–2

1974 ?*Dalmanella testudinaria* (Dalman); Lespérance, p. 12.

Description. Ventribiconvex. Dorsal sulcus faint. Hinge line narrow, equalling less than half maximum shell width which occurs near mid-length. Outline evenly rounded or slightly transverse. Largest individual 13 mm long. Ventral interarea apsacline; dorsal interarea anacline. Angular costellae increase in size anteriorly; new costellae originate through bifurcation. Four to six costellae in space of 2 mm measured 5 mm from beak. Cardinal process bilobed.

Material. Seven individuals were recovered.

Discussion. The bilobed cardinal process and external ornament are reminiscent of species of *Dalmanella* recorded in the Hirnantian fauna from other areas, but no identification can be made in the absence of specimens with the interiors preserved.

Family SCHIZOPHORIIDAE Schuchert and LeVene, 1929
Subfamily SCHIZOPHORIINAE Schuchert and LeVene, 1929
Genus HIRNANTIA Lamont, 1935
Hirnantia sagittifera (Mc'Coy, 1851)

Plate 109, figs. 3–11

1851 *Orthis sagittifera* M'Coy, p. 398.
1935 *Hirnantia sagittifera* (M'Coy); Lamont, p. 313, pl. 7, figs. 20–22.
1974 ?*Hirnantia sagittifera* (M'Coy); Lespérance, p. 12.

Exterior. Dorsibiconvex. Hinge line wide; maximum shell width slightly in front of cardinal extremities. Dorsal sulcus shallow, narrow, poorly defined. Costellae rounded in cross-section, much wider than interspaces. New costellae commonly originate through bifurcation but occasionally by intercalation. Three costellae occupy space of 1 mm measured 5 mm from beak. Very fine parvicostellae in interspaces (fila of Temple 1965). Parvicostellae and fine growth lines best preserved in outer moulds. Both interareas long, curved, laterally striate. Ventral interarea apsacline; dorsal interarea anacline.

Ventral interior. Teeth supported by strong dental plates diverging widely toward front. Low ridges extending short distance forward from dental plates bound muscle field. Weakly impressed muscle field confined to posterior quarter of valve. Adductor muscle scars occupy median third of muscle field, but extend forward only two-thirds length of diductor muscle scars. Adductor muscle scars bounded laterally by low, nearly parallel ridges. In addition, two very faint ridges are parallel to the sides of adductor muscle scars dividing them into equal thirds. Pedicle callist small, transversely striate. External ornament faintly impressed on internal surface.

Dorsal interior. Simple, bulbous cardinal process supported by high, short septum that continues anteriorly as very broad, rounded ridge extending to about mid-length. In one specimen minute septa lie on either side of cardinal process (Pl. 109, fig. 11). Similar septa in other schizophoriids were termed accessory cardinal processes by Schuchert and Cooper (1932, pl. A, fig. 14) and similar structures were found by Johnson (1970, pl. 9, fig. 13), in another species. Brachiophores tall; brachiophore support plates diverge anteriorly between 45 and 60 degrees. Sockets conical, supported by fulcral plates attaching directly to brachiophore supporting plates. Muscle field poorly preserved.

Material. Forty-one specimens were recovered including the interiors of ten dorsal and nine ventral valves.

Discussion. Small individuals of *H. sagittifera* can be distinguished from those of the small schizophoriid *Kinnella kielanae* by their much lower ventral valve, their dorsal interarea which is anacline rather than orthocline, and a weaker median ridge in the dorsal valve. *H. sagittifera* has been widely reported from the Hirnantian of Ireland, Great Britain, Poland, Sweden, Bohemia, and Morocco. Neuman (1968) reported *Hirnantia* sp. in Aroostook County, Maine.

H. noixella Amsden, 1974 from the Noix Limestone of Missouri is a very small species that differs from *H. sagittifera* in having costellae that are more rounded in cross-section and a more bulbous cardinal process. *H. noixella* does not grow large enough to develop the characteristic ventribiconvex valves of typical *Hirnantia* species (Amsden 1974). *H. senecta* (Hall and Clarke, 1892) from the Clinton Group of Reynales Basin, New York, and *H.* cf. *H. senecta* from the Brassfield Formation at Clinton, Tennessee, differ from *H. sagittifera* in having finer radial ornament, stronger ridges bounding the front of the ventral muscle field, a stronger dorsal median ridge, and better-defined dorsal muscle scars (see Walmsley *et al.* 1969).

Genus KINNELLA Bergström, 1968

Kinnella kielanae (Temple, 1965)

Plate 109, figs. 12–19

1965 *Hirnantia*? *kielanae* Temple, pp. 401–407, pl. 8, figs. 1–7; pl. 9, figs. 1–8; pl. 10, figs. 1–8; pl. 11, figs. 1–7; text-figs. 2*c–f*, 3*a–b*.
1968 *Kinnella kielanae* (Temple); Bergström, p. 11, pl. 4, figs. 3–6.
1974 *Kinnella kielanae* (Temple); Lespérance, p. 12.

Exterior. Shells ventribiconvex, ventral valve highly arched. Transverse, length about three-quarters width. Hinge line about two-thirds of maximum shell width, which occurs near mid-length. Dorsal sulcus shallow, poorly defined. Ventral interarea curved, apsacline, approaching catacline, very long, about half length of ventral valve. Dorsal interarea curved, orthocline, about one-third length of ventral interarea. Delthyrium very narrow. About four costellae in a space of 1 mm measured 5 mm from the ventral beak. Largest shell 9 mm long.

Ventral interior. Small, transversely striate pedicle callist. Teeth supported by anteriorly divergent dental plates. Broad, low ridges extending from front of dental plates surround muscle field. Muscle field confined to posterior half of valve. Diductor muscle scars enclose elongate adductor muscle scars.

Dorsal interior. Strong, broad median ridge extends from base of cardinal process to anterior margin. Adductor muscle scars reach well beyond mid-length, divided by faint transverse ridges into small posterior and much larger anterior portions. Muscle field bounded laterally by low, rounded ridges extending forward from bases of brachiophores. Tip of cardinal process not preserved. Sockets nearly parallel to hinge line.

Material. Twenty-four specimens were recovered including the interiors of three dorsal and three ventral valves.

Discussion. Specimens in our collections conform very closely to *K. kielanae* from Poland (Temple 1965), Great Britain (Temple 1965), Bohemia (Marek and Havlíček 1967), and Sweden (Bergström 1968). Temple (1965) suggested that this species may be conspecific with *Skenidium*? *medlicotti* Reed, 1915 from the 'Llandovery' of Panghsapye, Burma. Bergström (1968) noted several major differences between illustrated specimens of *S.*? *medlicotti* and *K. kielanae.*

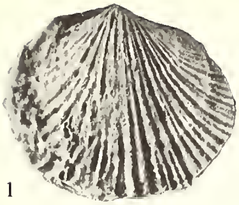
EXPLANATION OF PLATE 109

Figs. 1–2. *Dalmanella*? sp. 1–2, ventral and dorsal exterior of GSC 42216, ×2·0.

Figs. 3–11. *Hirnantia sagittifera* (M'Coy). 3–4, ventral and dorsal exterior of GSC 42217, ×2·5. 5, ventral exterior of GSC 42218, ×1·75. 6, ventral interior mould of GSC 42219, ×2·5. 7, ventral exterior mould of GSC 42220, ×2·5, fine growth lines present. 8, ventral interior mould of GSC 42221, ×2·5. 9, dorsal interior mould of GSC 42222, ×2·5. 10, dorsal interior mould with a fragment of the exterior shell surface of GSC 42223, ×2·5, fine growth lines faintly visible. 11, dorsal interior mould of GSC 42224, ×2·5, faintly showing minute septa lateral to the cardinal process.

Figs. 12–19. *Kinnella kielanae* (Temple). 12–13, posterior and dorsal exterior of GSC 42225, ×3·0. 14–15, posterior and lateral exterior of GSC 42226, ×3·0. 16–18, dorsal ventral and lateral views of interior mould of GSC 42227, ×3·0. 19, dorsal interior mould of GSC 42228, ×3·0.

Figs. 20–23. *Eostropheodonta siluriana* (Davidson). 20, dorsal exterior showing ventral interarea and chilidium, GSC 42229, ×1·75. 21, mould of part of the exterior ornament of dorsal valve, GSC 42230, ×5·0. 22, mould of the ventral exterior of GSC 42231, ×1·75. 23, dorsal exterior of GSC 42232, ×1·75.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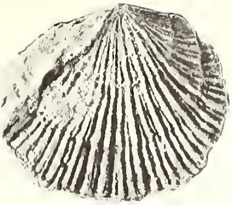
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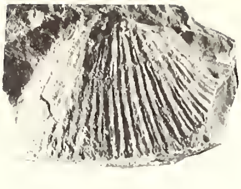
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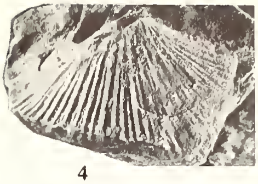
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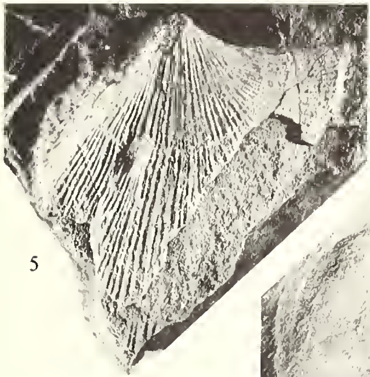
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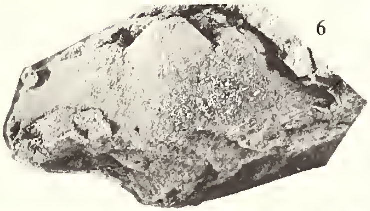
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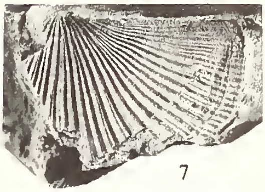
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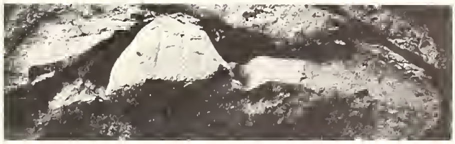
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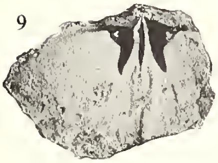
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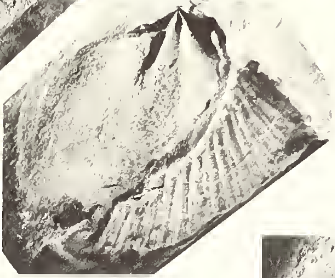
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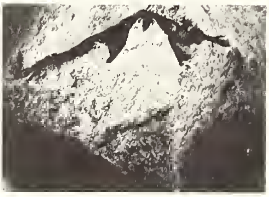
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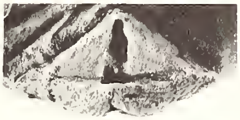
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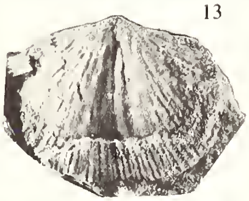
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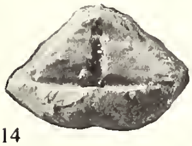
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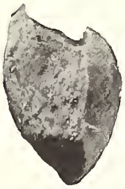
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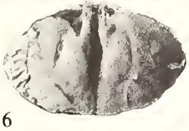
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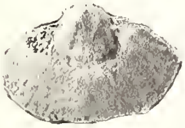
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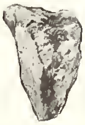
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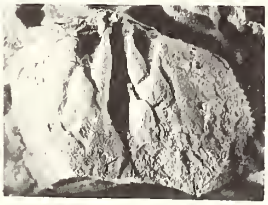
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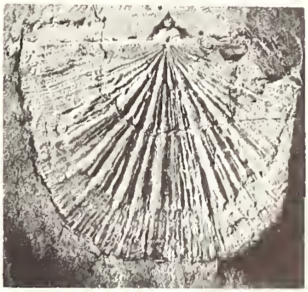
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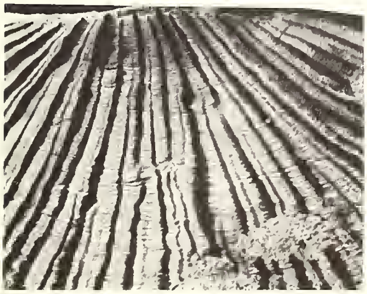
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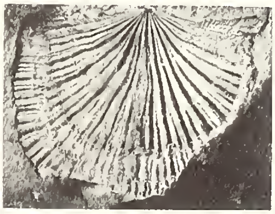
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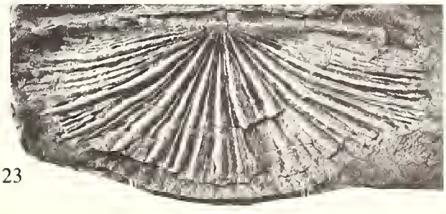
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LESPÉRANCE and SHEEHAN, *Hirnantia* fauna

Family EOSTROPHEODONTIDAE Havlíček, 1967
Genus EOSTROPHEODONTA Bancroft, 1949
Eostropheodonta siluriana (Davidson, 1871)

Plate 109, figs. 20–23; Plate 110, figs. 1–5

1871 *Strophomena Siluriana* Davidson, p. 303, pl. 47, figs. 1–4.
1953 *Stropheodonta* (*Eostropheodonta*) *siluriana* (Davidson); Williams, pl. 7, figs. 1–4.
1974 *Eostropheodonta hirnantensis* (Davidson); Lespérance, p. 12.

Exterior. Dorsal valve slightly concave; ventral valve somewhat more strongly convex. Maximum curvature about 5 mm from beak of both valves. Transverse; three shells were (*l*—18 mm, *w*—21 mm), (*l*—16 mm, *w*—19 mm), (*l*—20 mm, *w*—32 mm). Postero-lateral margins slightly mucronate. Fourteen to eighteen primary costellae originate near beak. Costellae bifurcate anteriorly, but primary costellae remain much stronger than new costellae, producing fascicostellate ornament. Costellae high, very steep sided, sharp-crested, and narrower than interspace. Costellae on postero-lateral margins weak. Commonly fourteen to sixteen costellae in space of 5 mm measured 5 mm from beak. Growth lines well defined, densely spaced. Anacline, nearly orthocline ventral interarea tall, gently curved laterally, nearly completely striate. Dorsal interarea catacline. Chilidium large, medially grooved with transverse striae. No deltidium.

Ventral interior. Dorsal facing surfaces of teeth antero-posteriorly striate. Teeth supported by short, thick dental plates diverging strongly toward front. No denticles observed. Flaring muscle field weakly impressed, bounded postero-laterally by dental plates and short low ridges extending forward from dental plates. Interspaces between costellae impressed on interior of valve forming low ridges; on crests of these ridges small tubercles (probably overlying pseudopunctae) most numerous anteriorly.

Dorsal interior. Only fragments of moulds of four dorsal interiors found. Bilobed cardinal process flanked by small socket plates. Slim blade between cardinal process lobes apparently supported chilidium. Short, low, broad ridge in front of cardinal process.

Material. Forty-five specimens were recovered including the interiors of four dorsal and eight ventral valves.

Discussion. Havlíček (1967) restudied *Eostropheodonta* and established the family Eostropheodontidae. Harper (1973) did not comment upon Havlíček's classification, but suggested that *Eostropheodonta* was possibly derived from a different ancestor than that of *Leptostrophia*, the first of the Stropheodontidae. If *Eostropheodonta* had a different ancestor from the stropheodontids, Havlíček's family Eostropheodontidae is consistent with the evolution of these groups.

The similarity of *E. siluriana* and *E. hirnantensis* has been commented on by Marr (1907), Elles (1922), and Wright (1968), who questioned the presence of two distinct species. The specimens under study are assigned to *E. siluriana* because of their very coarse fascicostellate ribbing. Wright (1968) suggested that the coarse ribbing may be related to the habitat as the ribbing pattern of *E. siluriana* is typically found in non-calcareous mudstones as is also the case here. The species need restudy; it may be that only a single species is present, but no intergradation between these two species (or morphotypes) is known, and they are treated as distinct with the data at hand.

E. hirnantensis from Sweden (Bergström 1968) differs from representatives of both species from other areas in lacking a median groove on the chilidium. Polish and Bala specimens of *E. hirnantensis* are distinguished by a faint fold and sulcus in the posterior of the shells (Temple 1965, and Université de Montréal collections). Havlíček (1971) proposed *E. squamosa* for specimens from Bohemia previously assigned to

E. hirnantensis; he also reported the species from the Ashgill of Morocco. This species, together with *E. jebilentensis* Havlíček (1971), *E. tafilaltensis* Havlíček (1971), *E. intermedia* Havlíček (1971), and *E. filicosta* Havlíček (1971) all from Morocco, can be distinguished from the species under study by their much finer costellae. *E. discumbata* Cocks and Brunton 1970 (in Cocks *et al.* 1970) from the late Ashgill or possibly lower Llandovery of South Africa differs from *E. siluriana* in having finer ornament, a narrower ventral muscle field, and in lacking a chilidium. *Rafinesquina*? *stropheodontoides* (Savage, 1913) is another weakly ribbed species which Amsden (1974) believes may be related to species of *Eostropheodonta*. *E. siluriana* has been reported previously only from the Hirnantian brachiopod fauna in the north of England; Wright (1968) notes its possible presence at Kildare, Ireland.

Family ANCISTRORHYNCHIDAE Cooper, 1956
Subfamily PLECTOTHYRELLINAE Bergström, 1968
Genus PLECTOTHYRELLA Temple, 1965
Plectothyrella crassicosta (Dalman, 1828)

Plate 110, figs. 6–21

1828 *Atrypa*? *crassicostis* Dalman, pp. 47–48.
1965 *Plectothyrella platystrophoides* Temple, pp. 412–415, pl. 20, figs. 1–5; pl. 21, figs. 1–10.
1967 *non Plectothyrella platystrophoides* (Temple); Marek and Havlíček, p. 284, pl. 1, figs. 14–17, 19.
1968 *Plectothyrella crassicosta* (Dalman); Bergström, p. 19, pl. 7, figs. 5–8.
1974 *Plectothyrella platystrophoides* Temple; Lespérance, p. 12.

Exterior. Ventribiconvex, transverse; no specimens well enough preserved to permit accurate length–width measurements. Dorsal fold, ventral sulcus, but in posterior 3–5 mm faint ventral fold and dorsal sulcus. Costae strong, angular, steep sided. Eight to ten costae on flanks. Costae on flanks originate near beak, do not bifurcate anteriorly. Two strongest costae on ventral valve bound sulcus. Median costa in sulcus. Eight to 10 mm from beak a weak costa is inserted on each side of median costa. A single atypical specimen has two costae the full length of the sulcus (specimen not illustrated). Dorsal fold formed by two strong costae bifurcating 12–15 mm from beak. Growth lamellae closely spaced, strongest anteriorly, best preserved in moulds. Hinge line wide for a rhynchonellid.

Ventral interior. Cyrtomatodont teeth small, bulbous. Dental plates converge basally, engulfed in secondary shell. Pedicle chamber in apex of shell and perched high above deeply impressed muscle field. Triangular muscle field expands anteriorly at about 30°, only faintly impressed in front. Adductor and diductor muscle scars not differentiated. Two grooves in muscle field parallel lateral margins of muscle field. Interspaces between costae strongly impressed as ridges in front of muscle field, but secondary shell lines posterior half of shell, obscuring impress of external ornament.

Dorsal interior. Cardinal process, crural plates, and inner hinge plates lacking. Sockets raised well above floor of valve, bounded by outer socket ridges and massive inner socket ridges. Crural bases large. Crura cylindrical, long, very large. High, narrow, median ridge set well in front of cardinalia, lower at mid-length, beyond which it is merely impress of median interspace of external ornament. Interspaces between costae strongly impressed on interior.

Material. Ninety-four specimens were recovered, including the interiors of eight dorsal, seventeen ventral, and six conjoined valves.

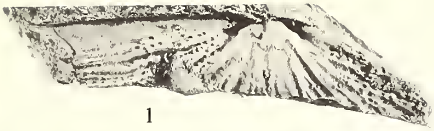
Discussion. The internal features of the dorsal valve are clearly rhynchonelloid, confirming Bergström's (1968) assignment of the genus to that order. Furthermore, Bergström's assignment of this genus to a separate subfamily within the Ancistrorhynchidae appears sound. Three species of *Plectothyrella* have been described: *P. crassicosta*, *P. haughtoni*, and *P. chauveli*. *P. haughtoni* from South Africa (Cocks *et al.* 1970) and *P. chauveli* from Morocco (Havlíček 1971) can easily be distinguished from *P. crassicosta* by their smaller, more numerous costae; *P. chauveli* also has a dorsal septalium. There is considerable morphologic variation within collections assigned to *P. crassicosta*, and the specimens under study fit well within the morphologic variability that has been described. The type specimen of *P. crassicosta* is from Sweden and specimens from Sweden usually have four costae in the sulcus (see Bergström 1968); there is but a single strong costa and two weaker ones in typical specimens from Percé. Specimens from Great Britain (see Temple 1965) more nearly resemble the Percé assemblage as they commonly have only three costae in the sulcus, but the ribs which form the dorsal fold bifurcate about 5 mm from the beak rather than at about 12–15 mm as in specimens from Percé. Bergström (1968) reports that specimens from Sweden have a dorsal median ridge that does not reach mid-length. English specimens have a dorsal median ridge that extends to the anterior margin (Temple 1965) as it does in specimens from Percé. The anterior portion of the ridge is, however, merely the impression of the median interspace, and there may be confusion as to whether or not it should be termed a median ridge.

The species has also been reported from the Hirnantian fauna from Kildare, Ireland (Wright 1968). Illustrated specimens assigned to the species from the Kosov Formation of Bohemia (Marek and Havlíček 1967) are quite distinctive and belong to a separate species. The Bohemian fossils have finer, more numerous costae (as many as fifteen costae on the flanks) than is known in *P. crassicosta*. In addition, some costae on the flanks bifurcate, and the fold and sulcus are not as well defined. Neuman (1968) reports that *Plectothyrella* sp. is present in Aroostook County, Maine. Bergström (1968) suggested that *Aratanea monodi* from ?Silurian rocks in the Sahara is similar to *P. crassicosta*. The species differs in having weaker ribbing and an elongate rather than transverse shell.

EXPLANATION OF PLATE 110

Figs. 1–5. *Eostropheodonta siluriana* (Davidson). 1, mould of ventral interior of GSC 42233, ×2·0. 2–3, enlargement of the mould of the hinge area showing striated teeth and the entire ventral interior mould of GSC 42234, ×5·0, ×2·0. 4, ventral interior of GSC 42235, ×1·75. 5, dorsal interior mould of GSC 42236, ×3·0.

Figs. 6–21. *Plectothyrella crassicosta* (Dalman). 6, dorsal exterior with a cornulitid, between two costae, left of centre, GSC 42237, ×1·5. 7, ventral exterior of GSC 42238, ×1·5. 8–9, posterior and lateral exterior of GSC 42239, ×1·5. 10–11, dorsal and ventral exteriors of GSC 42240, ×1·5. 12, posterior of GSC 42241, ×1·5. 13, posterior view of the inner mould of the conjoined valves of GSC 42242, ×1·75. 14, posterior view of the inner mould of the conjoined valves of GSC 42243, ×1·75. 15, posterior view of the inner mould of the conjoined valves of GSC 42244, ×1·75. 16, posterior view of a dorsal valve showing hinge sockets, inner socket ridges, and broken crura, GSC 42245, ×3·0. 17–19, ventral, dorsal, and lateral views of the internal mould of GSC 42246, ×1·75. 20–21, ventral inner mould and a lateral view of the same specimen, GSC 42247, ×1·75.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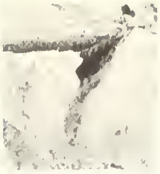
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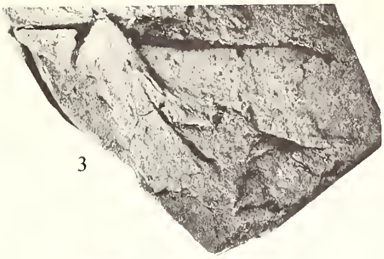
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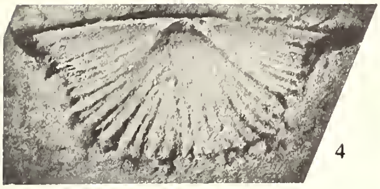
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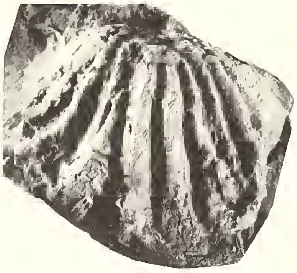
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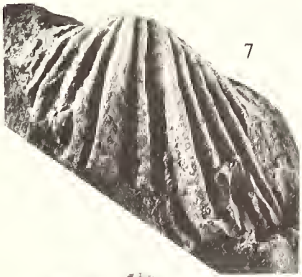
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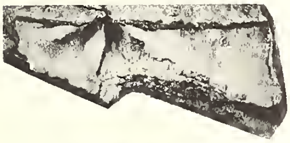
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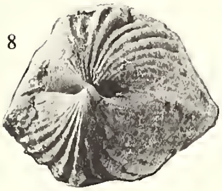
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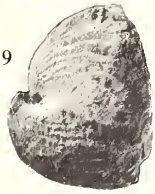
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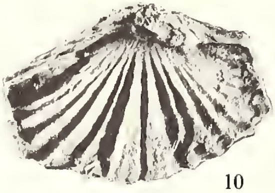
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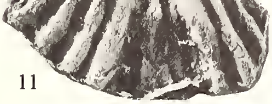
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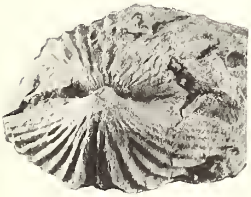
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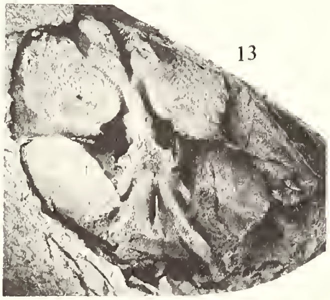
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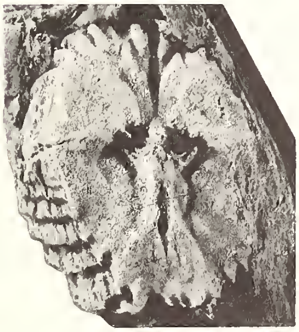
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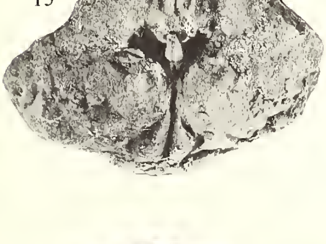
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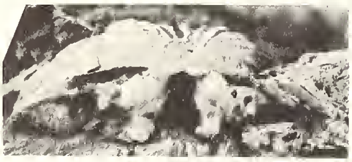
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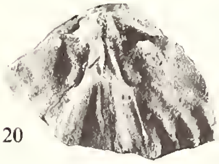
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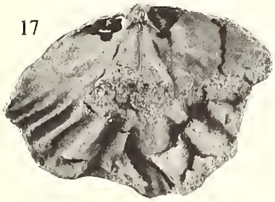
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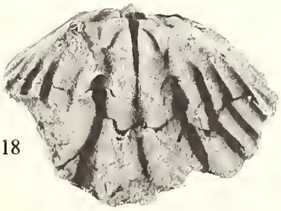
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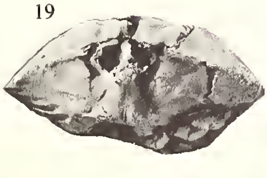
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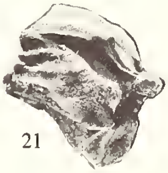
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LESPÉRANCE and SHEEHAN, *Hirnantia* fauna

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THE JURASSIC SELACHIAN FISH *PROTOSPINAX* WOODWARD

by J. G. MAISEY

ABSTRACT. *Protospinax* Woodward, 1919 (Kimmeridgian) is synonymous with *Belemnobatis* Thiollière, 1854, and is a rhinobatoid. The paratype of *P. annectans* Woodward, 1919 differs fundamentally from the holotype; it is described as *Squalogaleus woodwardi* gen. and sp. nov. and has galeoid-like jaws which lack an otic process. Primitive rhinobatoids and squatinoids have similar pectoral fin structure and a pectoral notch, suggesting a close primitive relationship.

WOODWARD (1919) proposed the name *Protospinax annectans* for two specimens in the British Museum (Natural History) from the Kimmeridgian of Bavaria. *P. annectans* is the only member of the family Protospinacidae Woodward, and the genus and family are always allotted an important position in elasmobranch phylogeny. *Protospinax* is the ancestor of batoids according to Woodward (1919); of batoids, squaloids, and orectoloboids according to White (1937) and Saint-Seine (1949); of squaloids according to Schaeffer (1967); and is possibly a transitional stage between squalomorphs and batoids according to Compagno (1973). A re-examination of the specimens has revealed new anatomical features including teeth and dermal denticles. The holotype (B.M. (N.H.) P.8775) is a rhinobatid referable to *Belemnobatis* Thiollière, 1854; the paratype B.M. (N.H.) 37014 is unique and represents a small, galeoid-like shark.

SYSTEMATIC PALAEONTOLOGY

Order EUSELACHIFORMES Maisey, 1975
Suborder RHINOBATOIDEA
Family RHINOBATIDAE Müller and Henle, 1938

Synonymy. Protospinacidae Woodward, 1919.

Genus BELEMNOBATIS Thiollière, 1854

Type species. *B. sismondae* Thiollière, 1854.

Belemnobatis annectans (Woodward, 1919)

Plate 111; text-figs. 1-4

1919 *Protospinax annectans* Woodward, p. 233, pl. I, figs. 2, 2*a non* figs. 3, 3*a*.

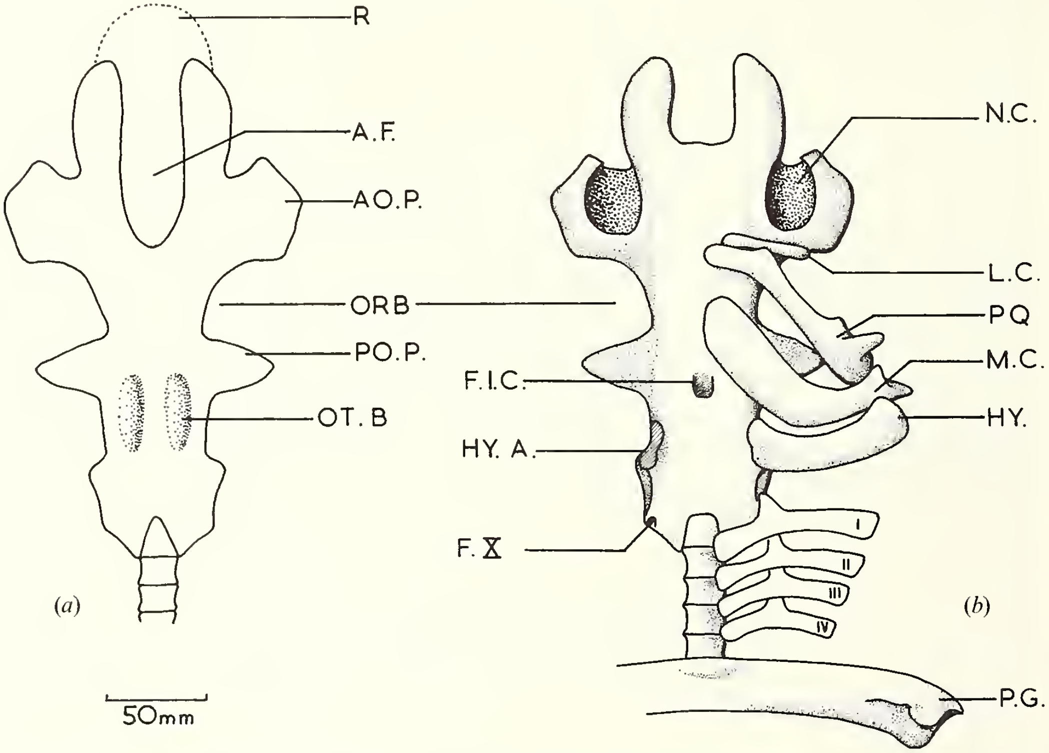
Diagnosis (emended). *Belemnobatis* with a short, obtusely rounded snout; cranial length to breadth ratio is 5:3, with the widest part at the antorbital processes; adult about 1·5 m long; the pectoral fins extend anteriorly almost to the otic region; a stout dorsal finspine projects from in front of each dorsal fin; the caudal fin is

[Palaeontology, Vol. 19, Part 4, 1976, pp. 733-747, pls. 111-112.]

deeply notched hypochordally; the lateral lines are supported by series of calcified ringlets.

Material. B.M. (N.H.) P.8775, the type specimen. Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich No. 1963-1-19.

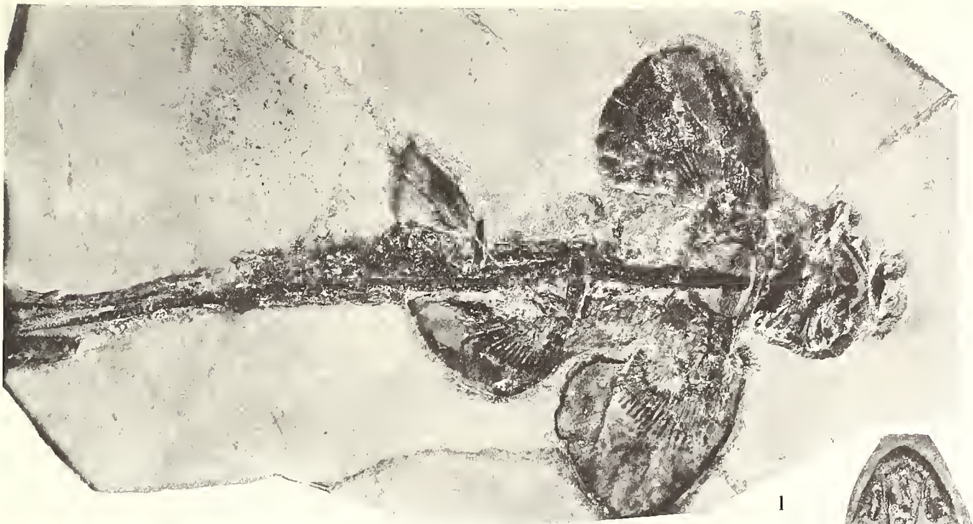
Description. The dorsal view of the braincase of the holotype (text-fig. 1*a*) shows nasal capsules, on either side of the anterior fontanelle, marking the broadest part of the rostrum. Impressions of these capsules are also visible in the Munich specimen. They are narrower where they meet the antorbital processes, but the anterior fontanelle is widest at this level. The antorbital processes mark the broadest part of the



TEXT-FIG. 1. Braincase and jaws of *Belemnobatis annectans* in (*a*) dorsal and (*b*) ventral views. Key to lettering: A.F., anterior fontanelle; AO.P., antorbital process; F.I.C., internal carotid foramen; F.X, foramen of tenth cranial nerve; HY, hyomandibular; HY.A., hyomandibular articulation on braincase; L.C., labial cartilage; M.C., Meckel's cartilage; N.C., nasal capsule; ORB., orbit; OT.B., otic bulla; P.G., pectoral girdle; PQ., palatoquadrate; PO.P., postorbital process; R., rostrum.

EXPLANATION OF PLATE 111

Figs. 1-3. *Belemnobatis annectans* (Woodward, 1919). 1, specimen 1963-1-19, Munich, as mounted on the wall of the Bayerische Stattssammlung für Paläontologie und historische Geologie, $\times\frac{1}{15}$ (B.S.P.H.G. photograph). 2, the same specimen; detail of the head and pectoral girdle, $\times\frac{1}{5}$ (B.S.P.H.G. photograph). 3, the holotype, B.M. (N.H.) P.8775, figd. Woodward (1919) entire fish, $\times\frac{1}{9}$ (B.M. (N.H.) photograph).



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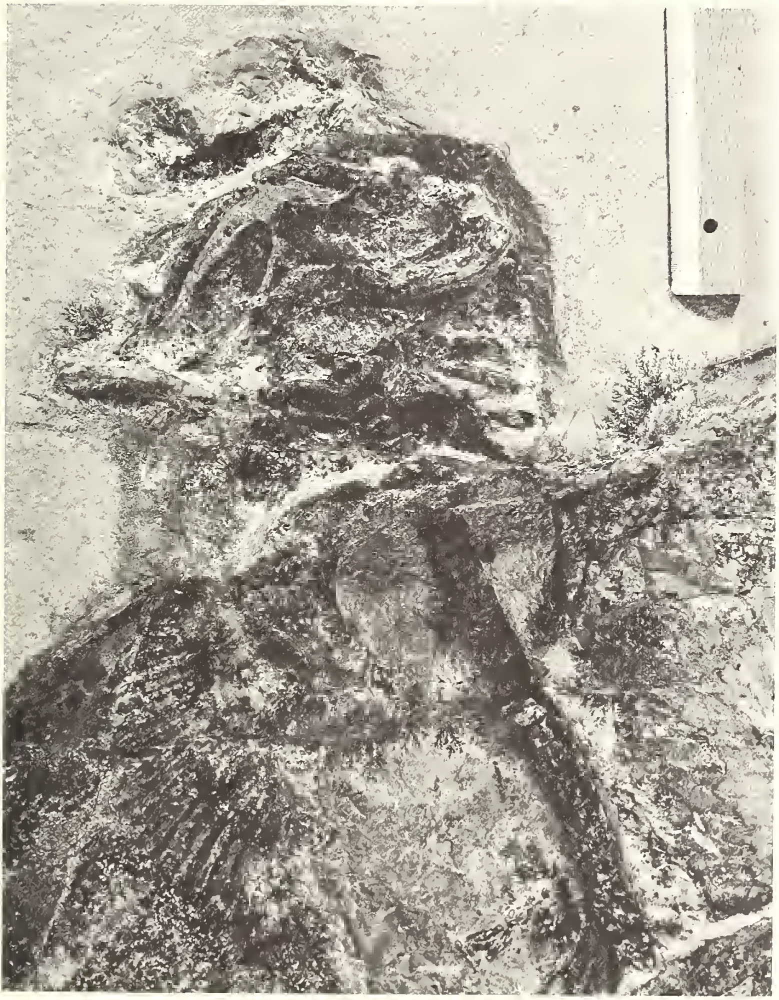

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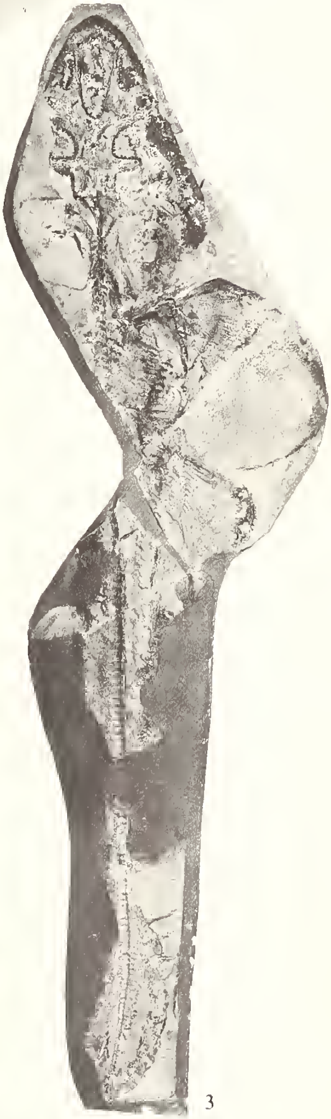

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MAISEY, *Protospinax*

head. They may have extended back further than is shown, as their posterior margins are broken in the holotype and are obscured by the jaws in the Munich specimen. These processes do not meet the propterygia. The orbits are not roofed by prismatic cartilage but are overlain by dermal denticles. There is no sign of a suborbital shelf. Postorbitally the braincase is long with large postorbital processes and a pair of otic bullae. On the posterior part of the basicranium of the Munich specimen, the internal carotid foramen is visible, immediately behind the jaws. A large hyomandibular facet upon the right otic process is also visible, the right hyomandibular being displaced slightly. A foramen, probably for the vagus nerve, is exposed on the right-hand corner of the braincase.

The palatoquadrates of the Munich specimen lie transversely beneath the orbits. They are unfused symphyseally and are thinner than Meckel's cartilages, tapering towards the symphysis. Meckel's cartilages have a double mandibular articulation (text-fig. 1*b*) and a narrow symphysis. The hyomandibulars (epihyals) are large and have a strong articulation with the braincase. The left hyomandibular is in place, and its distal extremity articulates with the mandibular arch at the jaw-joint. Ceratohyals are not visible and probably were absent originally. There is no trace of a 'pseudohyoid' (de Beer 1932). Four gill-arches are discernible in the Munich specimen. Epibranchial elements are visible posteriorly where deep excavation of the specimen is made. Further anteriorly, the ceratobranchials of these arches are visible. The gills probably opened ventrolaterally.

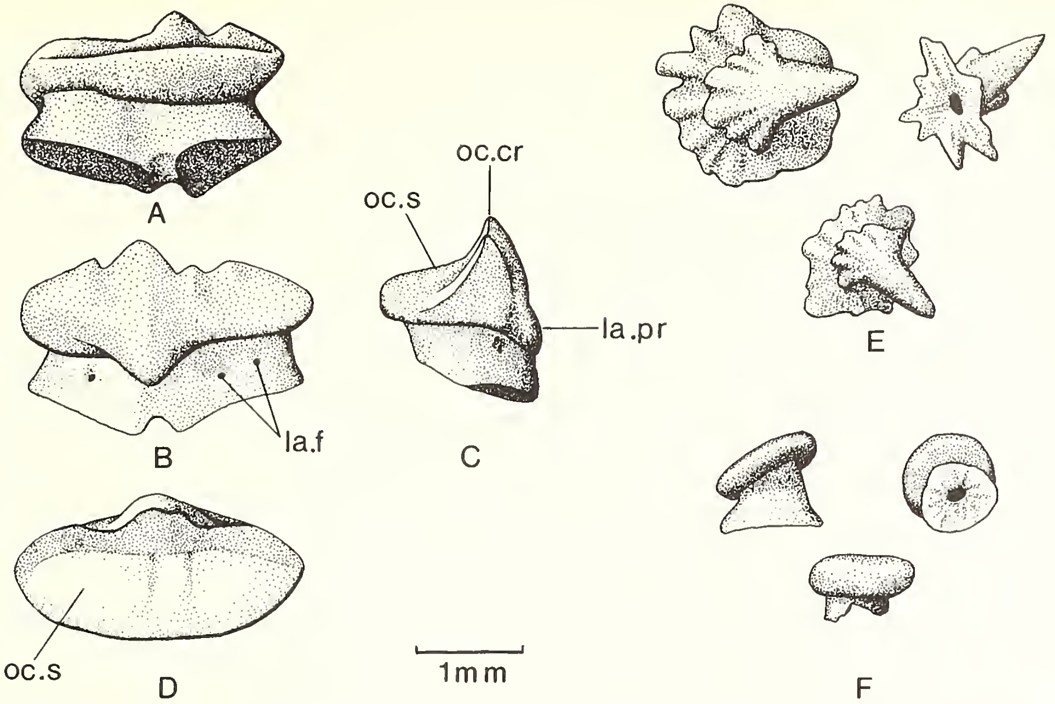
The teeth (visible in both specimens) are small (2–3 mm across). Their crowns have a flat occlusal surface (text-fig. 2A–D), raised labially into a low, moderately cuspidate occlusal crest. A labial coronal process extends over part of the root and is flanked by one or two pairs of foramina. The root is concave lingually, with a few lingual foramina. There is no lingual coronal process.

The coracoids are fused together ventrally, immediately behind the branchial arches. Large, posteriorly directed dorsal scapular elements are present. The pectoral fins are tribasal, but the shape of the propterygium is uncertain since it is damaged in the holotype and unexposed in the Munich specimen. Tips of the anteriormost propterygial radials lie near the otic region, but the propterygium ended further back. There is an anterior pectoral notch in the holotype (text-fig. 3). The pectoral outline differs between the specimens, partly because the pectoral fins are more widely spread in the Munich specimen (the outline of the left fin has been restored), and partly because the propterygia have not been prepared. In neither specimen are the pectoral fins smoothly confluent with the snout.

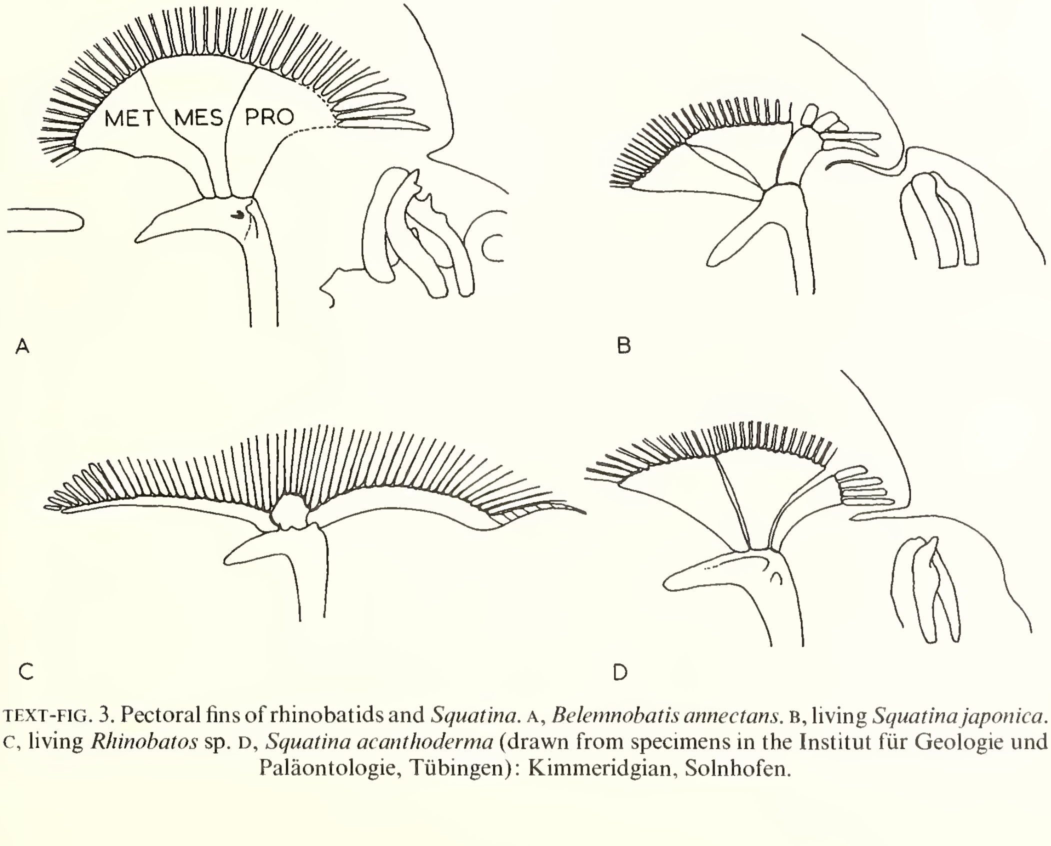
In outline, the meso- and metapterygia of the holotype and the Munich specimen are identical. The metapterygium is slightly attenuated posteriorly and carries fifteen radials. The mesopterygium is narrow proximally but is moderately broad distally and carries twelve radials.

Little can be added to Woodward's (1919) description of the pelvic fins. Their posterior margins are less elongate in the Munich specimen than in the holotype and claspers are absent, suggesting that it is a female. The pelvic girdle is a stout, transverse rod-like structure, lacking iliac or pubic processes.

The anterior dorsal fin has a short fissura posteriorly, but its endoskeleton is indistinct in both fossils. Its finspine is about 75 mm long and gently curved backward

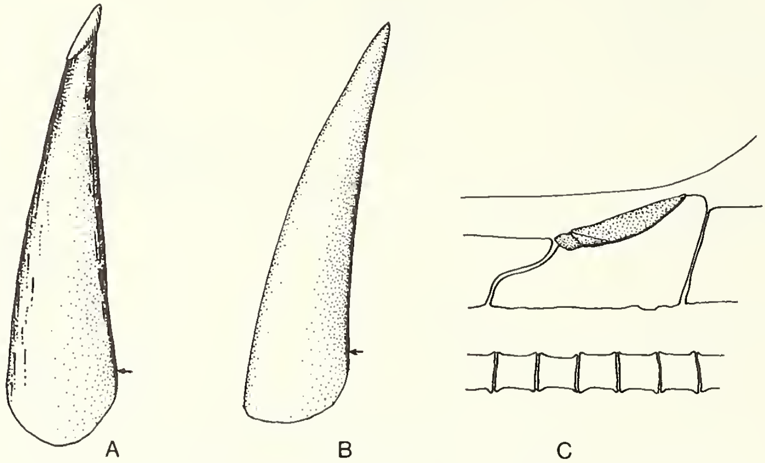


TEXT-FIG. 2. Teeth and scales of *Belemnobatis annectans*. A–D, tooth in A, lingual; B, labial; C, lateral; and D, occlusal views. Key to lettering: la.f., labial foramina; la.pr., labial process; oc.s., occlusal surface; oc.cr., occlusal crest. E, body scales. F, pharyngeal denticles.



TEXT-FIG. 3. Pectoral fins of rhinobatids and *Squatina*. A, *Belemnobatis annectans*. B, living *Squatina japonica*. C, living *Rhinobatos* sp. D, *Squatina acanthoderma* (drawn from specimens in the Institut für Geologie und Paläontologie, Tübingen): Kimmeridgian, Solnhofen.

in the Munich specimen. About 30 mm project from the body, and the spine is deeply inserted, with its base only 10 mm from the vertebral centra. The spine trunk is vascularized anteriorly and posteriorly but not basally. The level of posterior closure is moderately high. Only the tip of the spine is enamelled (text-fig. 4*a*). The unvascularized base of the anterior finspine is all that is present in the holotype.



TEXT-FIG. 4. Various rhinobatid finspines (not to scale). A, *Belemnobatis annectans* (from B.S.P.H.G. 1963-1-19, Munich). B, *Belemnobatis sismondae* (from Pi 1210/13, Tübingen). C, *Spathobatis bugesiacus* (from BM (N.H.) P.2099).

A second dorsal fin is present on the counterpart of the holotype, but no trace of a spine was found. In the corresponding position on the Munich specimen, traces of the second spine occur although the second dorsal fin has not been prepared. The posterior dorsal fin and spine are slightly smaller than the anterior.

The heterocercal tail has prominent epichordal and hypochordal lobes. Its hypochordal lobe is deeply notched, the anterior portion being interpreted as an anal fin by Woodward (1919). In fact, there is no anal fin.

The vertebral column has about 160 asterospondylous centra, each of which has several radial calcifications. Fossilized myotomal muscles occur down each side of the vertebral column in both specimens. A cervical synarcual is absent, but an occipital half-centrum is incorporated into the neurocranium between the occipital condyles.

Two patterns of scales occur. Small scales, with a multirayed, polygonal, or rounded base and flanged, acuminate crown, are present over most of the body (text-fig. 2E). Additionally, larger scales of similar shape are interspersed with the smaller ones dorsally. These scales have a more stellate base and a proximally lobate crown. A single foramen opens into each scale basally. The lateral lines are marked by a series of incomplete ringlets (Woodward 1919, pl. I, fig. 2*a*). These were not found on the Munich specimen.

Pharyngeal denticles have a rounded crown of polygonal outline, perched on a narrow pedestal. A median foramen opens into the denticle basally (text-fig. 2F). These scales were found on both specimens.

Affinities

Belemnobatis sismondae (Kimmeridgian of Bavaria and France) has been described by Thiollière (1854), Saint-Seine (1949), and Schweizer (1964). *B. annectans* closely resembles *B. sismondae* in tooth morphology, the forward limits of the pectoral fins, the position of the dorsal fins, the presence of a hypochordal finweb, the presence of a stout, projecting finspine, and the scale morphology. In other rhinobatids the teeth lack an occlusal crest, the pectoral fins extend to the snout, the dorsal fins are both posteriorly situated, there is no hypochordal finweb, finspines are reduced (*Spathobatis*) or absent, and the scales differ from those described here. *B. annectans* differs from *B. sismondae* in the relative anterior extent of the pectoral fins (to the orbits in *B. sismondae*), the presence of the pectoral notch, the stouter dorsal finspines which are enamelled, more deeply inserted, and lie closer to the dorsal fin in *B. annectans*, the relative depth and position of the hypochordal notch (deeper and more anterior in *B. annectans*), in the number of vertebral centra (about 150 in *B. sismondae*), and in the absence of ceratohyals.

The finspines of *B. sismondae* are completely unvascularized (specimen Pi 1210/13, figured by Schweizer 1964, pl. 11, figs. 1–3, was examined in Tübingen; both finspines are well preserved) and lack any trace of enamelled tissue (text-fig. 4*b*). In shape, cross-section, and in the presence of an anterior basal notch, these finspines resemble those of *B. annectans*. *Spathobatis* finspines (text-fig. 4*c*) lack enamelled tissue and are unvascularized, but are relatively smaller than in *Belemnobatis*. A morphological series can be postulated in which rhinobatid finspines progressively degenerated from partially vascularized, ornamented spines which projected from the body, to vestigial, unvascularized and unornamented spines which probably did not project from the body (text-fig. 4). This trend would appear to be a real one, since it agrees with earlier findings (Saint-Seine 1949) that *Belemnobatis*, *Spathobatis*, and *Rhinobatos* form a progressively more specialized series. In *Rhinobatos* finspines are absent.

The pectoral notch of *B. annectans* is unique in comparison with other rhinobatoids, but in *Squatina* the pectoral fins are similarly expanded (text-fig. 3). The pectoral basal of *B. annectans* closely resembles that of squatinoids and is not anteroposteriorly attenuated as in other rhinobatoids. Extension of the pectoral fins towards the head has produced the notch in both *B. annectans* and squatinoids. Similarities in the pectoral fins of *Squatina* and *B. annectans* may be phylogenetically significant; rhinobatoids could share a more shark-like common ancestor with squatinoids (see Compagno 1973, fig. 5). Rhinobatoids and squatinoids could therefore be early batoid sister groups. The absence of a synarcual and presence of an occipital half-centrum are primitive shark features; in other batoids a synarcual is present but the occipital half-centrum is absent (Compagno 1973). The squatinoid pectoral fin of *B. annectans* is probably primitive amongst rhinobatoids. No fossil squatinoid is known with finspines, and if squatinoids and rhinobatoids are primitively related, finspines were lost very early in squatinoid evolution.

Squatina is placed in the rays by Goodrich (1909) and Moy-Thomas (1939), but is placed apart by Garman (1913) and Compagno (1973). While there are many morphological differences between *Squatina* and other batoids, there is now less reason to separate them completely. I would place *Squatina* in a primitive sister-group to the Rhinobatoidea and other rays.

Order EUSELACHIFORMES Maisey, 1975

Suborder GALEOIDEA

(= Lamniformes + Carcharhiniformes *sensu* Compagno 1973)

INCERTAE FAMILIAE

Genus SQUALOGALEUS nov.

Diagnosis. Euselachians with degenerate dorsal finspines; an elongate neurocranium with a pronounced rostrum, a moderately long otic region; an elongate anterior fontanelle; the dentition is homodont around the jaw rami; dermal denticles are of two types, one having a simple unicuspid crown and a four-rayed stellate base, the other having a large conical crown and multi-rayed base, this type occurring only upon the head; adult about 270 mm long, with asterospondylous vertebrae.

Squalogaleus woodwardi gen. and sp. nov.

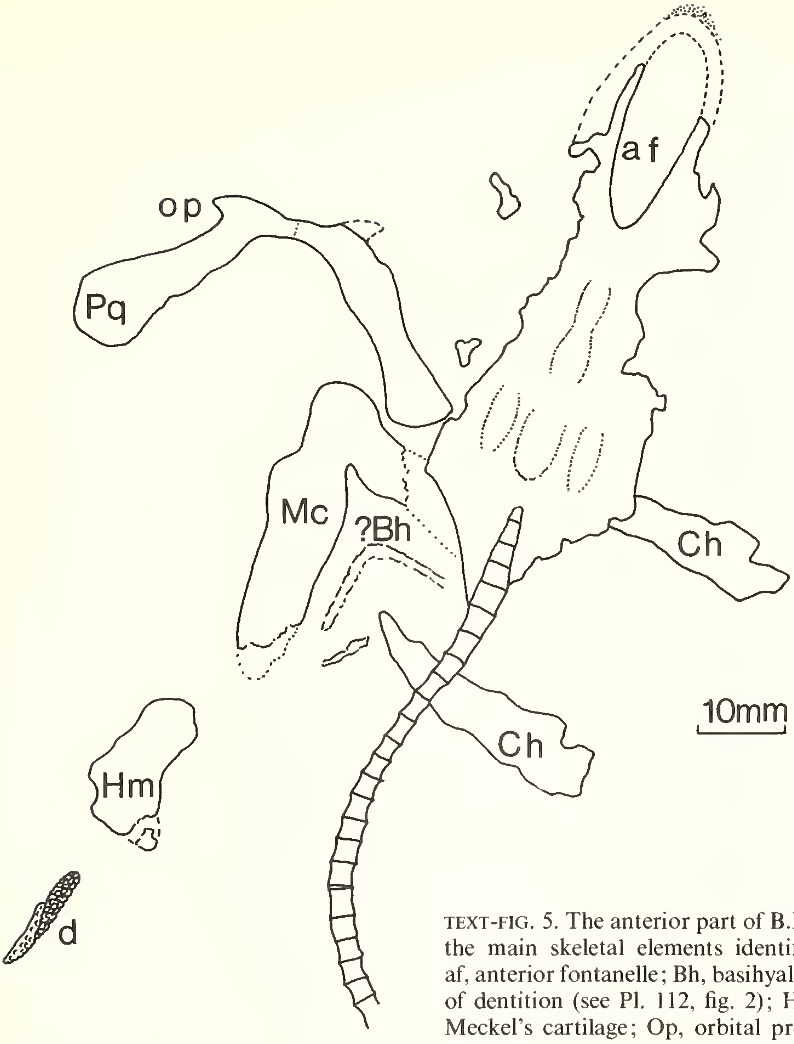
Plate 112, figs. 1–2; text-figs. 5–8

1889 *Cestracion falcifer* Wagner; Woodward (*partim*), p. 333.
1883 '*Acrodus*' Agassiz; Hasse, p. 66.
1919 *Protospinax annectans* Woodward, p. 233, pl. I, fig. 3, 3*a*.

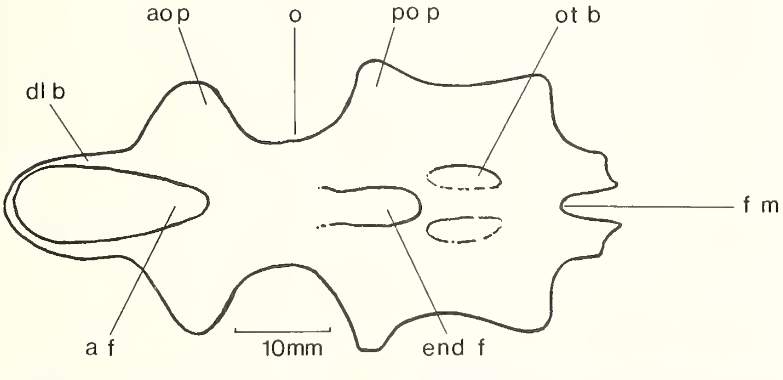
Diagnosis. Squalogaleus with low-cusped teeth having a labially offset crown and a prominent lingual process; tooth roots have one pair of lateral and single median lingual foramina, and two medial labial foramina; 109 vertebrae are present, the finspines overlying vertebrae 37–39 and 73–74.

Holotype. B.M. (N.H.) 37014, Kimmeridgian, from the Lithographic stone of Solnhofen, Bavaria: a unique specimen.

Description. The braincase of the holotype is dorsoventrally flattened and parts are missing, giving an asymmetrical outline (text-fig. 5). In the restored outline (text-fig. 6), prepared from superimposed normal and reversed drawings, the more damaged posterior region is conjectural. Processes on the otic region could therefore be longer, and the posterior margins of the braincase could be straighter. A long anterior fontanelle commences just anterior to the orbits and occupies one-third of the cranium length. The dorsolateral bars of the rostrum are thin, but are met by broad antorbital processes on each side of the anterior fontanelle. Postorbital processes mark the widest part of the cranium. Between them is an elongate depression, interpreted as the endolymphatic fossa. Behind the fossa, the long otic region bears a pair of low bullae. The occiput extends back to embrace the first three vertebrae laterally. No nerve foramina are exposed. The palatoquadrates are fused symphyseally and have a pronounced orbital process anteriorly, the prominence of which suggests a strong anterior connection between the jaws and the basicranium. Otic processes



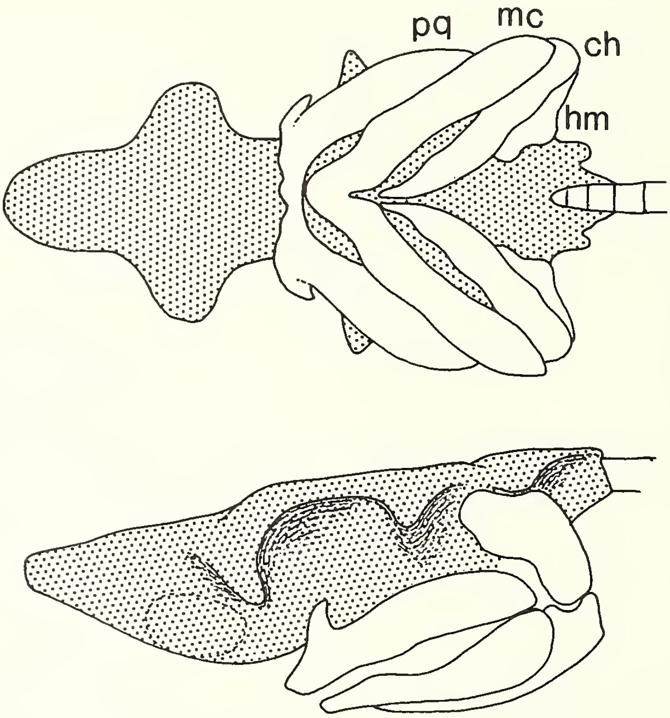
TEXT-FIG. 5. The anterior part of B.M. (N.H.) 37014 showing the main skeletal elements identified (cf. Pl. 112, fig. 1). af, anterior fontanelle; Bh, basihyal; Ch, ceratohyal; d, patch of dentition (see Pl. 112, fig. 2); Hm, hyomandibular; Mc, Meckel's cartilage; Op, orbital process of Pq; Pq, palatoquadrate.



TEXT-FIG. 6. Dorsal view of the braincase of *Squalogaleus woodwardi*. Abbreviations, as for text-fig. 1, plus dl b, dorso-lateral bar of rostrum; end f, endolymphatic fossa; f m, foramen magnum; o, orbit.

are absent from the palatoquadrates. The symphysis of Meckel's cartilages is stronger than that of the palatoquadrates.

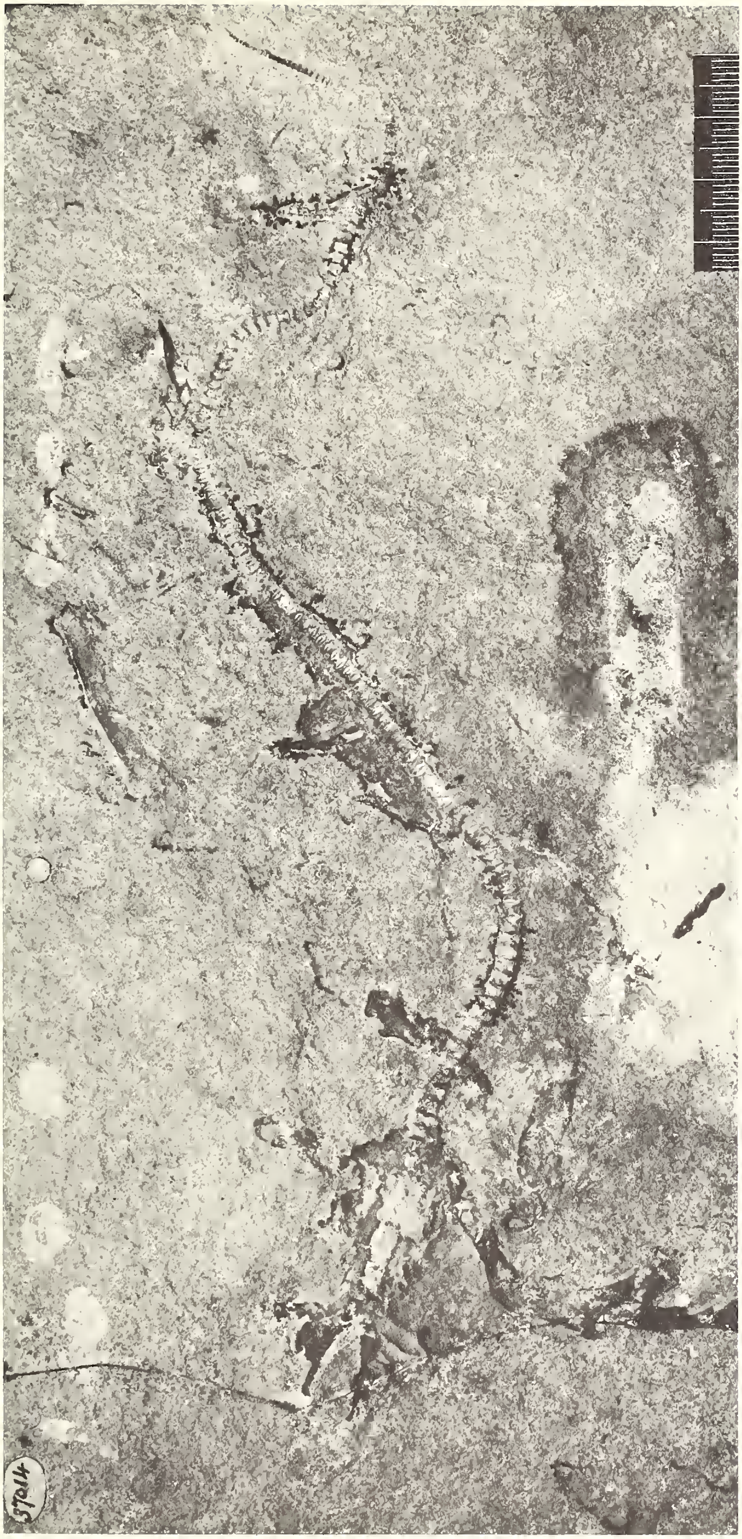
The ceratohyals are elongate and are moderately broad at their proximal (hyomandibular) end, tapering gradually towards the other end. There is a pronounced fossa for insertion of ligaments running from the hyomandibular. The ceratohyals are large in comparison with the jaw components, and probably terminated close to each other mesially. There is a small, chevron-shaped basihyal. The hyomandibular cartilages are large; the restored view of the mandibular and hyoid arches (text-fig. 7) shows the hyostylic suspension, with the hyomandibular cartilages meeting the mid-otic region of the braincase. The branchial arches are unknown.



TEXT-FIG. 7. Jaws of *Squalogaleus woodwardi* restored. ch, ceratohyals; hm, hyomandibular; mc, Meckel's cartilage; pq, palatoquadrate.

EXPLANATION OF PLATE 112

Figs. 1, 2. *Squalogaleus woodwardi* nov. 1, entire fish, B.M. (N.H.) 37014 (see text-fig. 5), ×0·84 (B.M. (N.H.) photograph). 2, part of lower dentition prepared in acid. To the left the teeth are inverted, exposing their roots; to the right the crowns are visible, ×9 (B.M. (N.H.) photograph).



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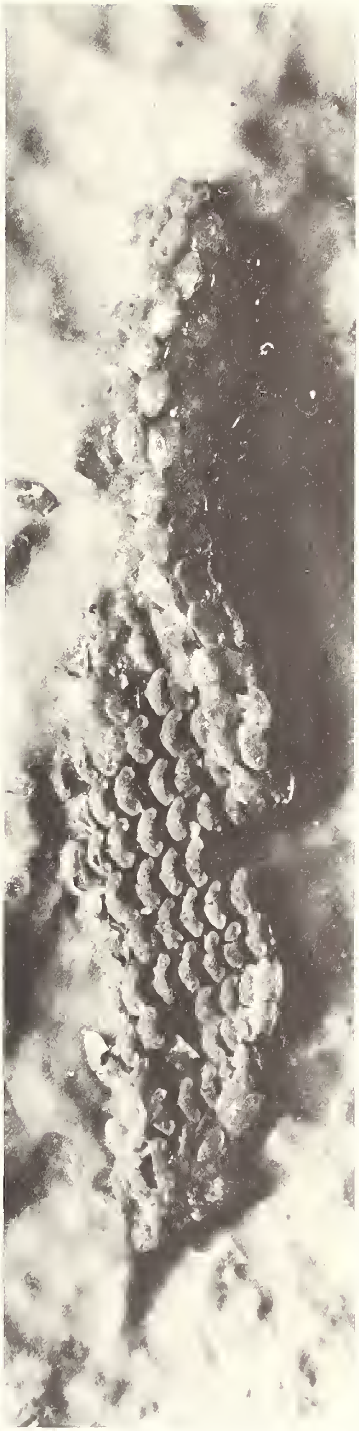

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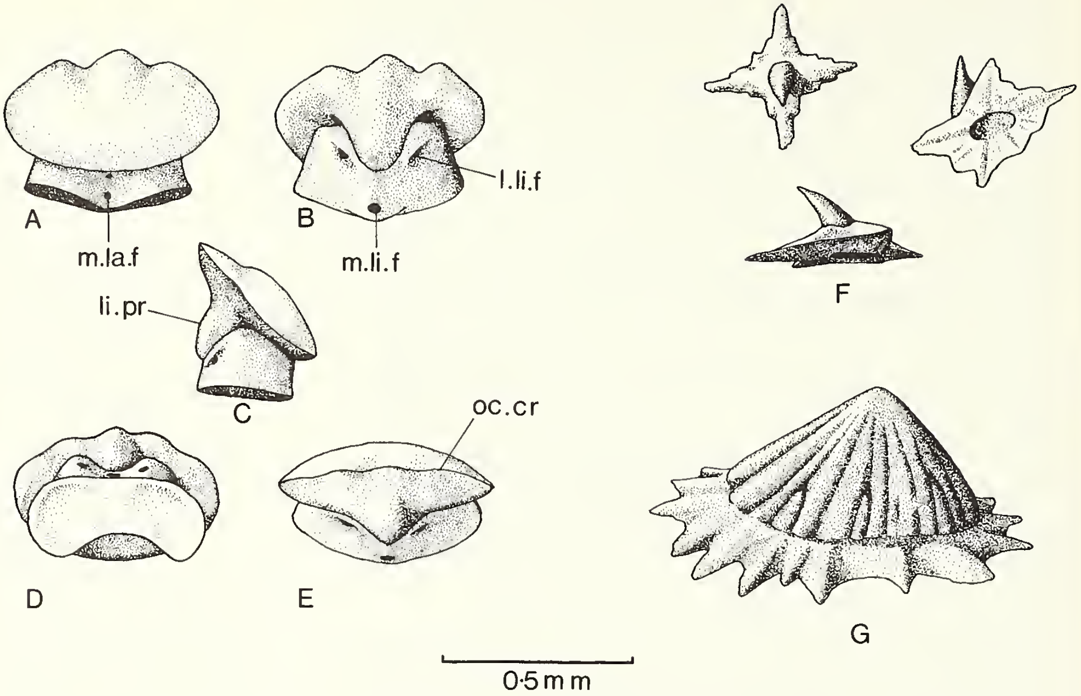
MAISEY, *Protospinax*



TEXT-FIG. 8. Tooth and scale morphology of *Squalogaleus woodwardi*. A–E, tooth in A, labial; B, lingual; C, lateral; D, basal; and E, occlusal views. Abbreviations: l.li.f, lateral lingual foramen; li.pr, lingual process; m.la.f, median labial foramen; m.li.f, median lingual foramen; oc.cr, occlusal crest. F, body scales. G, enlarged scale from head region.

The teeth (Pl. 112, fig. 2; text-fig. 8A–E) have smooth, enamelled crowns with a deep labial, but narrow lingual surface, a rounded median lingual process but no labial process. A longitudinal occlusal crest is invariably present. The only difference between anterior and lateral teeth is the degree to which their occlusal crest is raised into cusps; anterior teeth have slightly stronger median and lateral cusps than lateral teeth. The crown is offset labially on the root. Immediately below the lingual process is a median foramen, while to each side of the process is a lateral foramen. Labially there is one larger median foramen, above which a smaller one is situated. Lateral labial foramina occasionally occur. The root is crescent-shaped in basal view, with a labial concavity. Lingually the root is swollen below the coronal process. From six to ten teeth are present in each tooth replacement file. There is no significant difference in upper and lower dentitions. The teeth figured by Woodward (1919, pl. I, fig. 3) are from the upper dentition.

Two types of dermal denticles are present. Small (0·5 mm across) scales cover the body surface. Each scale has a four-rayed stellate base and an elongate, posteriorly recurved pointed crown (text-fig. 8F), which is enamelled. The pulp cavity is open basally. At least one pair of larger supraorbital scales is also present (text-fig. 8G) with a multi-rayed stellate base and a striated conical crown. No modified lateral line scales have been discovered.

Of the 109 vertebrae, the first eleven are simple double-cones with a length/breadth ratio of 1:1. The remainder are asterospondylous and have a length/breadth ratio of 2:3, with the vertebral diameter decreasing gradually towards the tail.

None of the fin skeleton is known, although the positions of the dorsal fins are deduced from the finspines, which are undisturbed. The finspines are round in section and are gently recurved posteriorly. The anterior spine is slightly the longer. Both finspines are deeply inserted, terminating basally just above the vertebral column. Neither finspine is enamelled, and both are composed of lamellar dentine, through which numerous dendritic odontoblast canaliculi radiate from the spine central cavity. The finspine trunk has a double-layered structure.

Affinities

Woodward (1919) regarded B.M. (N.H.) 37014 as a juvenile selachian, but he failed to recognize the almost complete lower dentition (Pl. 112, fig. 2) showing fully developed and closely spaced replacement files. Replacement files of juvenile sharks are widely spaced and have few teeth per file (Daniel 1928; Smith 1940). The fully calcified braincase also suggests an adult specimen.

The primitively phalacanthous order Euselachiformes here includes the fishes grouped by Compagno (1973) into the superorders Squalomorphii, Batoidea, Squatinomorphii, and Galeomorphii; i.e. the modern representatives of his 'Cohort Euselachii', but excluding hybodonts and ctenacanths (see Maisey 1975). Within such a framework, *Belemnobatis annectans* is a primitive batoid, displaying a primitive squatinomorph pectoral fin. *Squalogaleus woodwardi* differs from *B. annectans* in its cranial morphology, jaw arrangement, teeth, the number of vertebrae, the position and relative size of the finspines, the lack of lateral line ringlets in *Squalogaleus*, and in the scale morphology. Additionally *Squalogaleus* is considerably smaller than *B. annectans* and it is concluded that *B. annectans* and *Squalogaleus* are profoundly different. *S. woodwardi* differs from other rhinobatoids in the same ways that it differs from *B. annectans*, and is probably not closely related to them (or to batoids generally). The finspines are rounded in cross-section, in common not only with rhinobatoids, but also with *Oxynotus* (Squalidae; Maisey 1974).

Although *S. woodwardi* resembles heterodontid and squalid euselachians in possessing finspines, this primitive feature does not necessarily indicate heterodontid or squalid affinity. The nonvascular condition of modern squalid, heterodontid, certain fossil rhinobatid, and *S. woodwardi* finspines probably arose independently, because earlier euselachians (such as *Palaeospinax* and some fossil heterodontids) had vascularized finspines (Maisey 1975). The absence of enamelled tissue on *S. woodwardi* finspines is probably degenerate; finspines of *Oxynotus*, *Euprotomicrus*, and some fossil rhinobatids similarly lack it, and these forms are closely allied to others in which finspines are absent. *S. woodwardi* is unlikely to have been ancestral to either spinate squaloids or heterodontoids, but is more probably related to some group of anacanthous euselachians.

Squalomorphs and heterodontiform and orectolobiform galeomorphs (*sensu* Compagno 1973) primitively retain a palatoquadrate otic process (Holmgren 1940, 1941). This is lost in *S. woodwardi* and in Compagno's (1973) other galeomorphs (here termed the suborder Galeoidea), except for the uniquely amphistylic *Pseudocarcharias*.

This form may stem from a different branch of primitive galeoid stock to *Squalogaleus*; in one, the otic process was retained but finspines were lost; in the other, the otic process was lost although finspines were (for a while) retained.

S. woodwardi does not possess the downturned ethmoidal region characteristic of heterodontids or orectolobids. Its cranial morphology shows some squaloid features, such as the elongate rostrum, the depth of the anterior fontanelle, and the position of the endolymphatic fossa, but all these may be primitive euselachiform features. The otic region of *S. woodwardi* is considerably longer than in modern selachians, even than in *Heptranchias*. A long otic region is also found in many primitive fossil selachians (hybodonts, ctenacanths, cladodonts), and the braincase of *S. woodwardi* represents a generalized pattern which could have predominated in many early euselachians.

Squalogaleus differs from living and fossil orectolobids (e.g. *Orectolobus*, *Palaeocarcharias*) in not having enlarged lower symphyseal teeth, an apparently primitive orectolobid feature (Compagno 1973). Its tooth roots have few foramina, unlike the multiforaminate teeth of very primitive euselachians (*Palaeospinax*, *Synechodus*, *Orthacodus*) and the finspines are unvascularized. *Squalogaleus* is unlikely to be closely related to such early forms.

Squalogaleus is regarded as a primitive, spinate galeoid euselachian principally because the palatoquadrate otic processes are lost. It may lie close to a divergence of squalomorphs (*sensu* Compagno 1973) and galeoids. Also it may differ from early squaloids only in lacking palatoquadrate otic processes and enamel upon the finspines.

Acknowledgements. I thank Dr. C. Patterson of the British Museum (Natural History) for his assistance; Professor Dr. Dehm and Dr. Wellnhofer of the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, for allowing me to examine the second specimen of *Belemnobatis annectans*; and Dr. W. E. Reif for showing me the *Belemnobatis* and squatinoid fossils at the University of Tübingen. The work forms part of a study of spinate chondrichthyans for a Ph.D. thesis, which was supported by a Science Research Council Studentship. Subsequent study of the Munich and Tübingen specimens was made possible by an award given by the British Council and the Deutscher Akademischer Austauschdienst.

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Note added in proof. The finspines of *Breviacanthus* Maisey, 1976, a Bathonian finspine genus of primitive rhinobatoid affinity, have a partly vascularized trunk like those of *Belemnobatis annectans*, but are more extensively ornamented.

MAISEY, J. G. 1976. The Middle Jurassic selachian fish *Breviacanthus* n.g. *N. Jb. Geol. Paläont. Mh.* **H. 7,** 432–438.

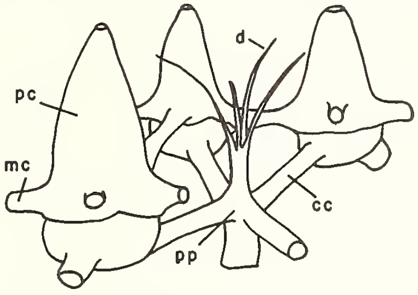
PLEROMIC DENTINE IN A PERMIAN CROSSOPTERYGIAN FISH (FAMILY OSTEOLEPIDAE)

by KEITH S. THOMSON

ABSTRACT. Pleromic dentine is reported filling the pore-cavity spaces within the cosmine of the Early Permian rhipidistian fish *Ectosteorhachis nitidus* Cope (Family Osteolepidae). The pleromic tissue is only found in regions of specialized cosmine where the regular pattern of seasonal resorption and regeneration has broken down—a process that occurs in the later life history of members of this species. The functional significance of the pleromic tissue seems to be mechanically to reinforce these regions of more permanent cosmine, with minimal loss of function in the pore-canal sensory system.

THE dermal skeleton of many early fishes bears an external layer of dentine or dentine-like material usually covered with 'enameloid'. In this respect these lower vertebrates differ significantly from the higher groups in which dentine-like and enamel-like materials are confined to the dentition. The exact configuration of the dentine layer on the dermal skeleton of early fishes varies from group to group, but a widely distributed pattern is termed *cosmine*. Cosmine (see, for example, Gross 1956 and Thomson 1975) is characterized as a compound set of tissues including an enamel-like material, dentine, and a small amount of true spongy bone, all surrounding the mosaic pore-canal system. The pore-canal system is a sensory system consisting of a series of neuromast ampullae contained in conical pore-cavities opening to the surface at minute pores and which connect with each other via mesh-canals (text-fig. 1; for full description, see Gross 1956 and Thomson 1975).

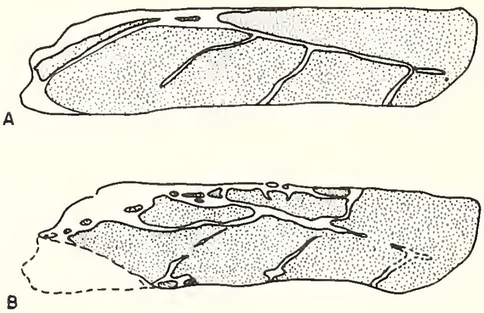
Little is known about the developmental biology of cosmine. In a recent study (Thomson 1975) it appears that the following features can be established with some certainty. The ontogenetic formation of hard tissues cannot proceed without association with the pore-canal system. Normally, the cosmine is renewed seasonally (see Westoll 1936 for first discussion of the biology of cosmine). In most Dipnoi and in osteolepid Rhipidistia, formation of new cosmine occurs only after the complete resorption of the old cosmine (for the sole exception, see the description of 'superficial blisters' by Jarvik 1950). In the case of local trauma to the cosmine, local resorption occurs, leaving a bare patch in a cosmine sheet, the margins of which are raw and 'unfinished'. Over this bare patch a new 'inserted blister' of cosmine may be formed as a discrete area with smoothly rounded, finished margins. The evidence of



TEXT-FIG. 1. Schematic view of the arrangement of pore-canal system and pulp cavities in *Ectosteorhachis nitidus*. cc, cross canal; d, dentine tubules; mc, mesh canal; pc, pore cavity; pp, pulp cavity.

[Palaeontology, Vol. 19, Part 4, 1976, pp. 749–755, pl. 113.]

this may persist through later phases of resorption and renewal in the form of a ring-shaped scar with fully finished margins. In *Ectosteorhachis*, there exists an apparently unique situation whereby the process of seasonal renewal breaks down during the life history, so that most adult fish no longer possess a full external covering of cosmine. Instead, the cosmine is reduced dorsally to a series of prominent tubercles along the back and sides of the head and one large tubercle on each scale of the dorsal and dorso-lateral scale rows. In the ventro-lateral parts of the body, the dermal skeleton remains covered with a continuous covering similar to that found for a longer time in other osteolepids and in lungfishes. Eventually, however, while the gular series may continue with a full cosmine cover, the mandibles show only a partial cover, consisting of isolated patches of cosmine with finished margins, and considerable expanses of bare dermal bone (text-fig. 2).



TEXT-FIG. 2. Diagrammatic representation of the extent of cosmine cover in two mandibles of *Ectosteorhachis nitidus*. In A a more or less complete cover is maintained, showing some gaps along the dermal bone sutures. In B a less complete cover exists, with many small 'islands' of cosmine surrounded by bare dermal bone. Cosmine areas stippled. (Based on two specimens from the Museum of Comparative Zoology at Harvard University, MCZ 8927a and MCZ 8927b.)

The purpose of the present note is to record a novel modification of the cosmine in the Early Permian crossopterygian fish *Ectosteorhachis nitidus* Cope. In material of this species, evidence has been found of the formation of *pleromic dentine*. Pleromic dentine has been described and defined by Tarlo and Tarlo (1961) as a form of dentine secondarily filling vascular and other spaces in superficial parts of the skeleton in certain fossil fishes. The term is also used in this strict sense by Denison (1973) although Orvig (1967) has used it more generally to denote hypermineralized dentine. In fact, the first description of pleromic dentine seems to have been that of Kiaer (1915) who demonstrated the production of new dentine, apparently in response to wear, in the dermal armour of psammosteids. Gross (1930, 1935) also discussed the phenomenon, as did Bystrov (1955) and Halstead (for review see Halstead-Tarlo 1965 and Halstead 1969). Subsequently, Gross (1971) has described similar pleromic dentine in acanthodians.

In the course of study of the cosmine in *Ectosteorhachis*, pleromic dentine was found filling certain pore-cavities of the pore-canal sensory system. In the extensive

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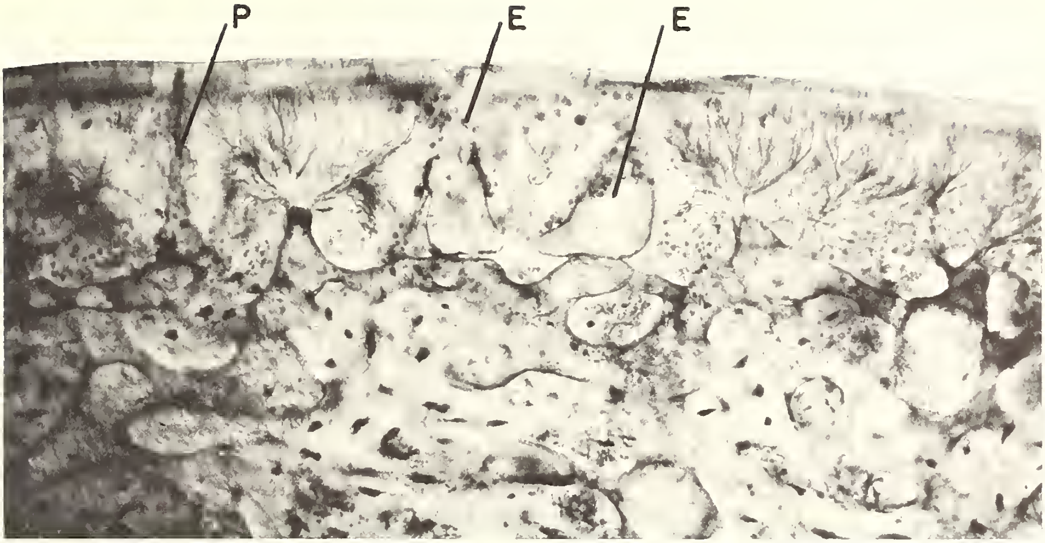
EXPLANATION OF PLATE 113

Vertical thin-sections through the cosmine of the mandible of *Ectosteorhachis nitidus* (MCZ 13350). A, section showing three pore-cavities and several sets of dentine tubules. The pore-cavity marked P is filled with pleromic dentine (see enlargement in text-fig. 3E). The pore-cavities marked E are normal (i.e. empty). ×approx. 80. B–F, five sections showing the detailed arrangement of the pleromic dentine within pore-cavities from the mandible. × 160. G, enlargement showing a pore-cavity from a 'tubercle' with pleromic dentine. The pulp cavity of the pleromic dentine shows as a dark elongated mass in the centre of the in-filled pore-cavity. × 160.



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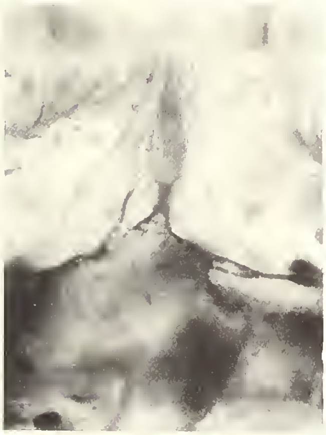

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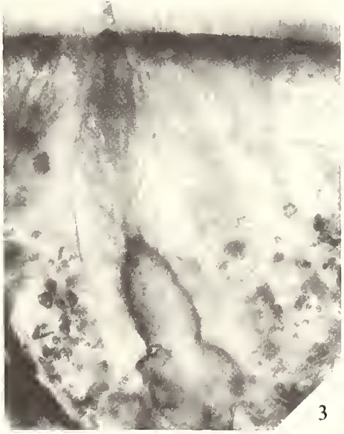

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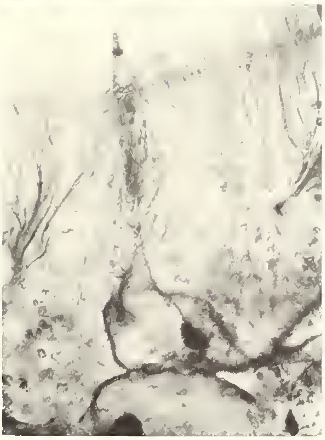

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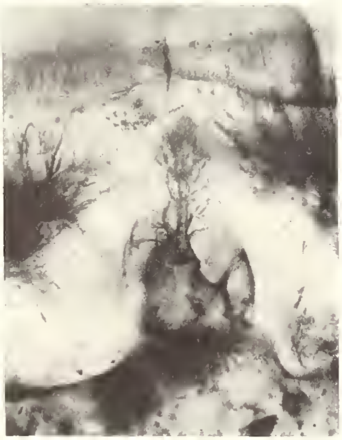

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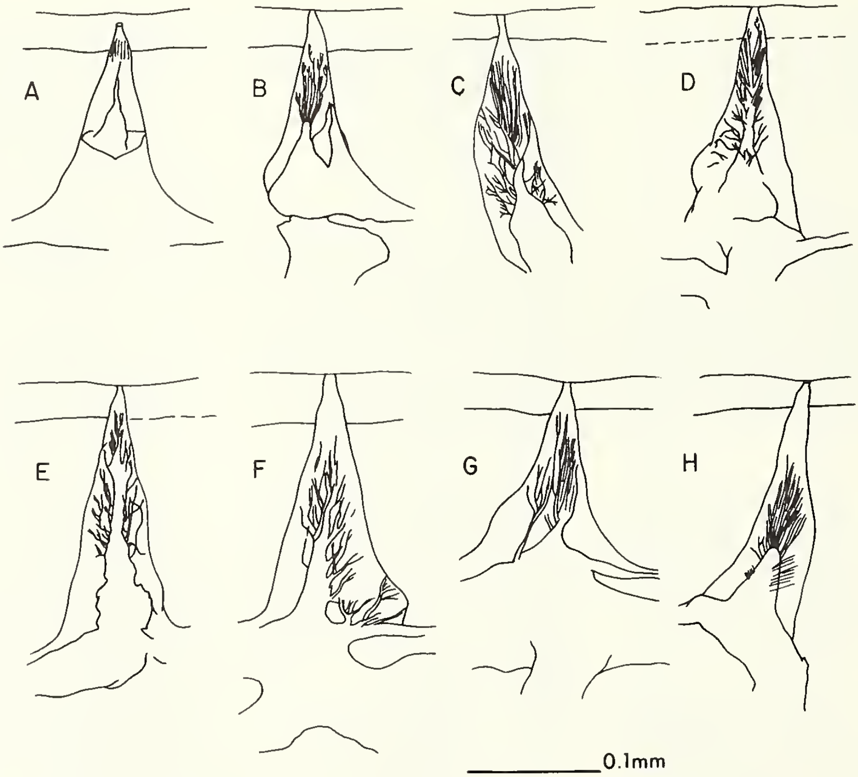
THOMSON, Pleromic dentine

suite of material of *E. nitidus* that was studied, pleromic dentine was found in all tubercles that were sectioned, and in one portion of a mandible in a late stage in the breakdown of the cosmine covering. Pleromic dentine was never found in more than 80–90% of the pore-cavities in any particular region. In some cases open (and therefore presumably fully functional) pore-cavities were observed next to fully filled ones (Pl. 113). Pleromic dentine was not found in the standard continuous sheets or in blisters.

The pleromic tissue does not seem to extend into the cross-canals and in only one case has it been found in the basal chamber of a pore-cavity (text-fig. 3F; Pl. 113, fig. C). Within each affected pore-cavity, there is one or occasionally two pulp-cavities for the pleromic tissue and in some cases we can observe pulp-cavities in different stages of formation (text-fig. 3A, B). The pleromic dentine tubules are of exactly the same diameter as the dentine tubules of the surrounding cosmine, but their pattern of radiation is naturally constrained by the conical shape of the pore-cavity, and the pulp-cavity is of very different shape among the various examples seen. In the pleromic dentine of the tubercles, there are relatively few dentine tubules and



TEXT-FIG. 3. Drawings of the pleromic dentine filling the pore-cavities in cosmine of the mandible of *Ectosteorhachis nitidus*. In each case the outline of the pore-cavity is shown, with the pattern of branching dentine tubules and central pulp cavity of the pleromic dentine.

the pulp-cavity has a basically cylindrical form, contrasting with the more conical pulp-cavity with profusely branching dentine tubules that is seen in the pleromic dentine in the mandibular fragment. The pleromic dentine seems to be highly mineralized. In the case of the tubercles, the pleromic tissue is hypermineralized, as is the somewhat trabecular dentine of the original cosmine.

The biological significance of the pleromic dentine described here is difficult to determine. The two most likely possibilities are that the pleromic tissue occurs in response to physiological factors such as local trauma or pathological conditions, or that it represents an adaptive modification of cosmine structure for greater durability. Local physiological effects might include loss of function of the pore-cavity ampullae, but it seems more probable that mere damage to the soft tissue of a sensory ampullae would be repaired readily. Under normal conditions local damage to any part of the hard tissue would result in resorption and formation of a blister (see Thomson 1975). On the other hand, if a given cosmine region normally had a life expectancy of approximately one year before seasonal replacement, then breakdown in the pattern of cosmine replacement in the later stages of the history would require each cosmine surface to last much longer. Pleromic dentine formation has the effect physically of reinforcing the cosmine in proportion to the number of pore-cavities filled in. Thus we can perhaps explain the formation of pleromic dentine as an adaptation to increase the durability of the cosmine, which is made necessary by a two-fold age-related change in the cosmine. First, the cosmine is not fully replaced on a seasonal basis and second, the cosmine is reduced to a series of localized patches separated by bare dermal bone on the surface of which are soft tissues. If the pore-canal system remains fully developed in the soft tissues, its partial loss from those small areas still covered with cosmine can be tolerated. A mosaic system like the pore-canal system could probably withstand the loss of some 10–20% of sensory ampullae over all, and up to 90% in localized regions, without major impairment of function. Thus the tubercles and remaining flat patches of cosmine came to be composed of a cosmine from which functional pore-canal ampullae were gradually lost and which was progressively reinforced with pleromic dentine as the fish aged. The extent of the development of the pleromic tissue in a given region of a particular specimen will therefore reflect both the age and 'life expectancy' of that piece of cosmine. Such an explanation would also account for the absence of pleromic dentine from other lobe-finned fishes in which a complete cosmine cover is normally maintained by seasonal replacement.

The formation of dentine requires an inductive interaction between preodontoblast cells (probably of neural crest origin in most lower vertebrates) and the epidermis. When the cosmine was seasonally resorbed, a new epidermis and reorganized dermis containing the intact pore-canal system were the site of new cosmine formation, as odontoblasts were organized beneath the epidermis and ameloblasts organized in the basement membrane. In some fishes, such as the holoptychoid Rhipidistia (see, for example, *Porolepis*, in Ørvig 1967), new layers of cosmine were laid down on top of the old, and in this case we must assume overgrowth of soft tissues superficial to the existing cosmine, prior to the new phase of deposition. Superficial cosmine blisters of the sort described by Jarvik (1950) for osteolepids and Denison (1973) among others, for heterostracans, can be explained in the same way.

The occurrence of the pleromic dentine in *Ectosteorhachis* raises some problems with respect to an epidermal contribution. First, the pleromic dentine is topographically interspersed within, rather than outside, the existing dentine and is thus internal to the original site of the epidermal layer. Secondly, because not all the pore-canal system in the relevant region is filled in with pleromic dentine, we must assume that the process of dentine formation did not interfere with the remaining functional sensory units. Thirdly, there is no sign of modification of the rest of the hard tissues.

If the cosmine in *Ectosteorhachis* were covered normally with a thin layer of epidermis, through which the pore-canal system opened, then the situation could easily be explained. New odontoblasts could be organized in the superficial soft tissue and enter the pore-cavities through the external pores, in direct response to loss of function and resorption of the sensory tissues. However, it is normally assumed that such an epidermal layer is absent and, if one had been present, it would have been subject to extensive wear and tear. There are two alternatives to account for the formation of pleromic odontoblasts. First, one could assume that there was a very localized and specific overgrowth of the surface by epidermal tissues, allowing new dentine formation in the pore-cavities but not interfering with the operation of the rest of the pore-canal system. A second possibility is that the odontoblasts concerned were sequestered in an inactive form within the cosmine, having been induced with the mass of odontoblasts that laid down the original cosmine. These cells were then activated as a result of local events in the vascularized tissues at the base of the dentine as each pore-cavity became inactive and its contents resorbed. Such an occurrence has not previously been suggested, but it cannot be completely ruled out. The question can hardly be settled at this far remove from the actual events. Whether the new odontoblasts entered the pore-cavity from the external opening or through the basal vascular system, we can envisage the formation of a plug of pulp tissues within which the odontoblasts became organized in a superficial layer and then migrated centripetally as hard tissue formation progressed.

In summary, the formation of pleromic dentine in the pore-cavities of the cosmine of *E. nitidus* is an age-related phenomenon that is probably an adaptation serving to increase the durability of the cosmine. As the cosmine surfaces are being reduced in area, the resulting loss in function of the pore-canal system is minimized. The developmental origin of the new dentine is uncertain.

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A NEW SPECIES OF *CORVASPIS* (AGNATHA, HETEROSTRACI) FROM THE UPPER SILURIAN TO LOWER OR MIDDLE DEVONIAN OF THE NORTH-WEST TERRITORIES, CANADA

by E. J. LOEFFLER *and* D. L. DINELEY

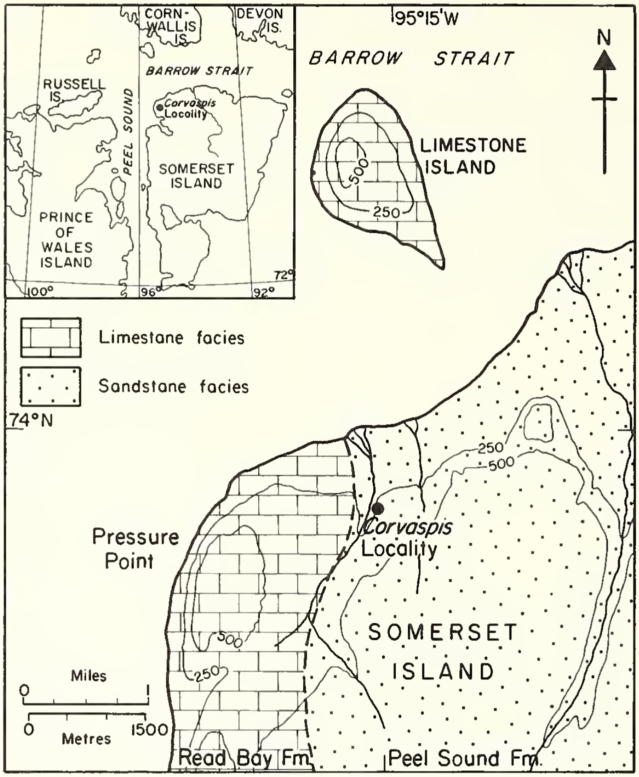
ABSTRACT. A new species of *Corvaspis*, *C. arctica*, is described from the Peel Sound Formation of Somerset Island, North-west Territories, Canada, where it occurs in association with *Hemicyclaspis murchisoni* (Egerton), an index fossil for the lowest Downtonian of Britain. *C. arctica* sp. nov. is considered to have been a streamlined form, with an undivided dorsal shield; it is probably related to the Cyathaspididae.

DURING the mid 1960s a large amount of ostracoderm material was collected from the Peel Sound Formation of Somerset and Prince of Wales Islands in Arctic Canada by members of the University of Ottawa (Dineley 1965*a* and *b*, 1966*a* and *b*). Detailed descriptions of much of this material have now been published (Dineley 1968 and in press; Broad and Dineley 1973; Broad 1973), or included in theses (Broad 1968, 1971). Of the remaining material, three specimens of *Corvaspis* have been selected for description here because they contribute to the continuing debate on the affinities of the genus.

The three specimens (NMC 21600–21602) were collected in 1965 by one of the authors (D. L. D.), from a band of white sandstone approximately 12 m above the floor of a stream gorge, immediately east of the hill at Pressure Point, on the north-western tip of Somerset Island (text-fig. 1). The same locality also yielded two articulated specimens of *Hemicyclaspis murchisoni* (Egerton), large and small cyathaspidids, traquairaspidids, and acanthodians (Dineley 1968). *H. murchisoni* is regarded as an index fossil for the lowest Downtonian of Britain (White 1950); such a stratigraphic designation (now accepted as equivalent to the early Pridolian Stage) was considered by Dineley (1968) as in accord with the position of the ostracoderm horizon, which is an estimated 15–18 m above the base of the Peel Sound Formation. This locality is approximately 20 km west of that from which Thorsteinsson and Tozer (in Fortier *et al.* 1963) reported two new genera of cyathaspidid, one of which was said to compare favourably with *Corvaspis* (ibid., p. 122); these specimens have not yet been figured or described.

The specimens described below represent only a small part of the *Corvaspis* material present in the collections from Somerset Island, or indeed from the same locality; fragmentary *Corvaspis* plates occur in a blotchy sandstone unit 3 m lower in the section. No attempt is made here to describe the rest of the material from this locality; it includes orbital, lateral, and medial fragments, which vary in size and ornamentation, but contribute little to our knowledge of *Corvaspis*.

[Palaeontology, Vol. 19, Part 4, 1976, pp. 757–766, pl. 114.]



TEXT-FIG. 1. Locality map.

SYSTEMATIC PALAEONTOLOGY

The ostracoderms with which this paper is concerned are the property of the National Museum of Canada, Ottawa, and bear the catalogue numbers (prefixed NMC) of that institution.

Order HETEROSTRACI Lankester, 1868
Family CORVASPIDIDAE Dineley, 1953
Genus CORVASPIS Woodward, 1934
Corvaspis arctica sp. nov.

Plate 114; text-figs. 2–4

Derivation of name. The specimens are from Arctic Canada.

Diagnosis. Dorsal shield long (90 mm) and narrow (width ratio = 0·44), completely enclosing orbits. Ornamentation of short (1–10 mm), closely spaced, smooth-topped, dentine ridges, 0·2–0·5 mm wide and of uniform height. Superficial units, 1·0–3·0 mm long and 1·0–4·0 mm wide, produced by local grouping of dentine ridges; anterior units with peripheral ridges curved around median ridge, posterior units scale-like, and intermediate units with parallel ridges.

Holotype. NMC 21600, incomplete dorsal shield (Pl. 114, fig. 1; text-fig. 2).

Other material. NMC 21601 (Pl. 114, fig. 2; text-fig. 3); NMC 21602 (Pl. 114, fig. 3; text-fig. 4), incomplete dorsal shields.

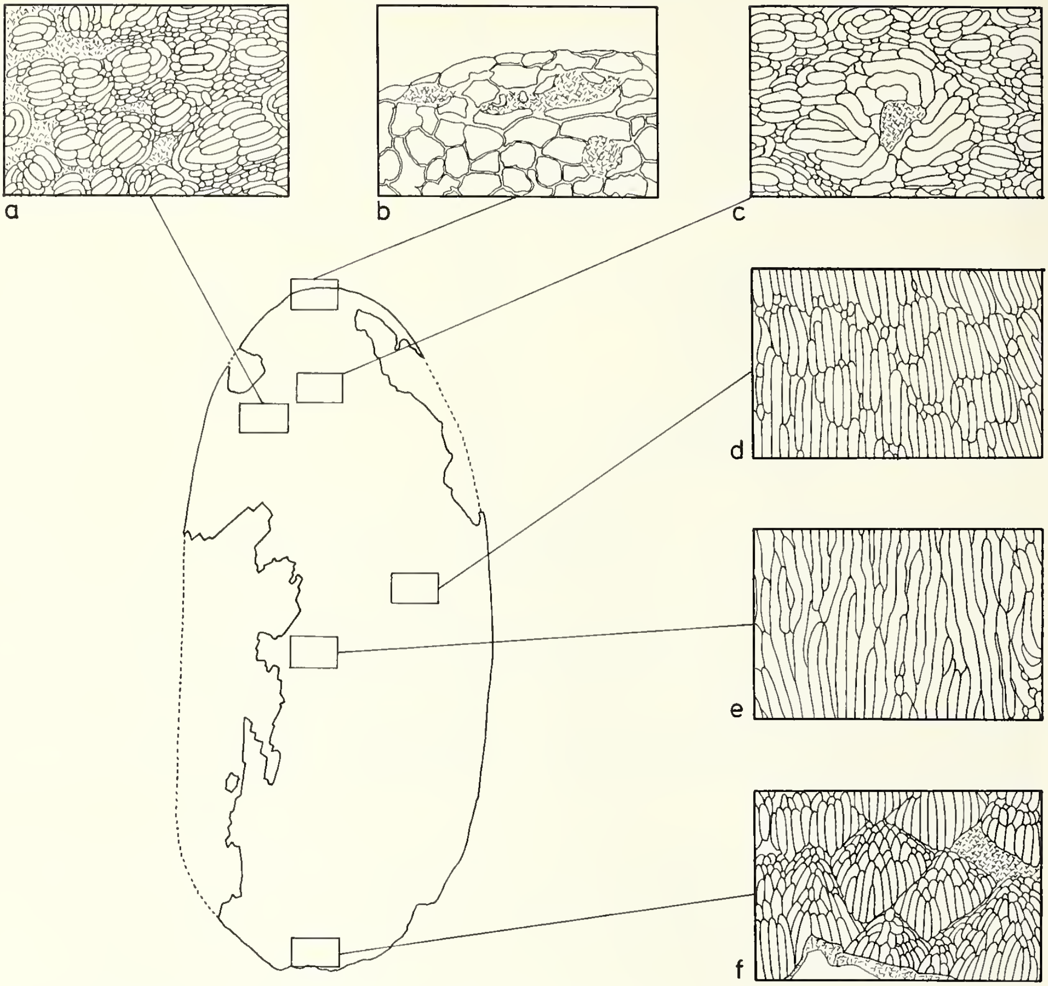
Locality. 12 m above floor of gorge east of Pressure Point, N.W. Somerset Island.

Description. Dimensions of dorsal shields (using those parameters measured by Denison (1966) in the Cyathaspididae):

	NMC 21600	NMC 21601
Median length	90 mm	—
Maximum width	40 mm	—
Pineal length	14 mm	—
Orbital width	21 mm	21 mm
Orbital length	9 mm	7 mm
Width ratio	0·44	—
Pineal length ratio	0·16	—
Orbital width ratio	0·23	—
Orbital length ratio	0·10	—

The long, narrow dorsal shield has a smoothly rounded rostral margin and an irregular posterior margin. The pineal macula, which is well preserved in NMC 21602, but abraded in the holotype, is situated slightly behind the interorbital line. The orbits are small (diameter 2·5 mm), circular, and anteriorly placed (Pl. 114, fig. 2); although close to the lateral margin of the shield, the eyes appear to have been dorsally, rather than laterally, directed. In the holotype and in NMC 21601, the lateral margins of the shield are underturned to form a ventro-lateral lamina extending back from the preorbital region; owing to the friable state of the skeletal material, preparation of these laminae proved impossible. No branchial lobes, notches, or openings are apparent.

Ornamentation is of uniformly high, closely spaced dentine ridges which are commonly less than 3 mm long; their local grouping into small units, separated by grooves or by rows of tubercles, produces a superficial subdivision of the shield (Pl. 114, figs. 1–3). This subdivision is absent from the rostral and lateral margins of the shield, around the orbits, and locally on the central part of the shield. The character of the units changes throughout the length of the shield. In the anterior third, each unit comprises peripheral ridges which are curved or grouped around a single median ridge (text-fig. 2*a*); divisions between the units are not very distinct, and the orientation of the median ridge varies widely. Within the posterior third of the shield, units are distinctly scale-like (text-figs. 2*f* and 3*b*). Each is in the form of a rhomb, approximately 1·5 × 1·5 mm, within which tubercles are placed in front of short ridges, in an arrangement similar to that of the detached body scales which are associated with the holotype (Pl. 114, fig. 1). The gradation from scale-like units to true body scales, at the posterior end of the headshield, makes the precise shape of the posterior margin of the shield uncertain. In the intervening part of the shield, between the anterior units with curved peripheral ridges and the posterior scale-like units, the ridges are only locally grouped into units. Where units are present, they comprise short (up to 3 mm), parallel ridges with a longitudinal arrangement (text-figs. 2*d*, 3*c*). In the absence of such units (text-fig. 2*e*), ridges vary in length up to a maximum of 10 mm.



TEXT-FIG. 2. *Corvaspis arctica* sp. nov. Variation in ornamentation of dorsal shield NMC 21600 (holotype). Plan ×2, detail ×12.

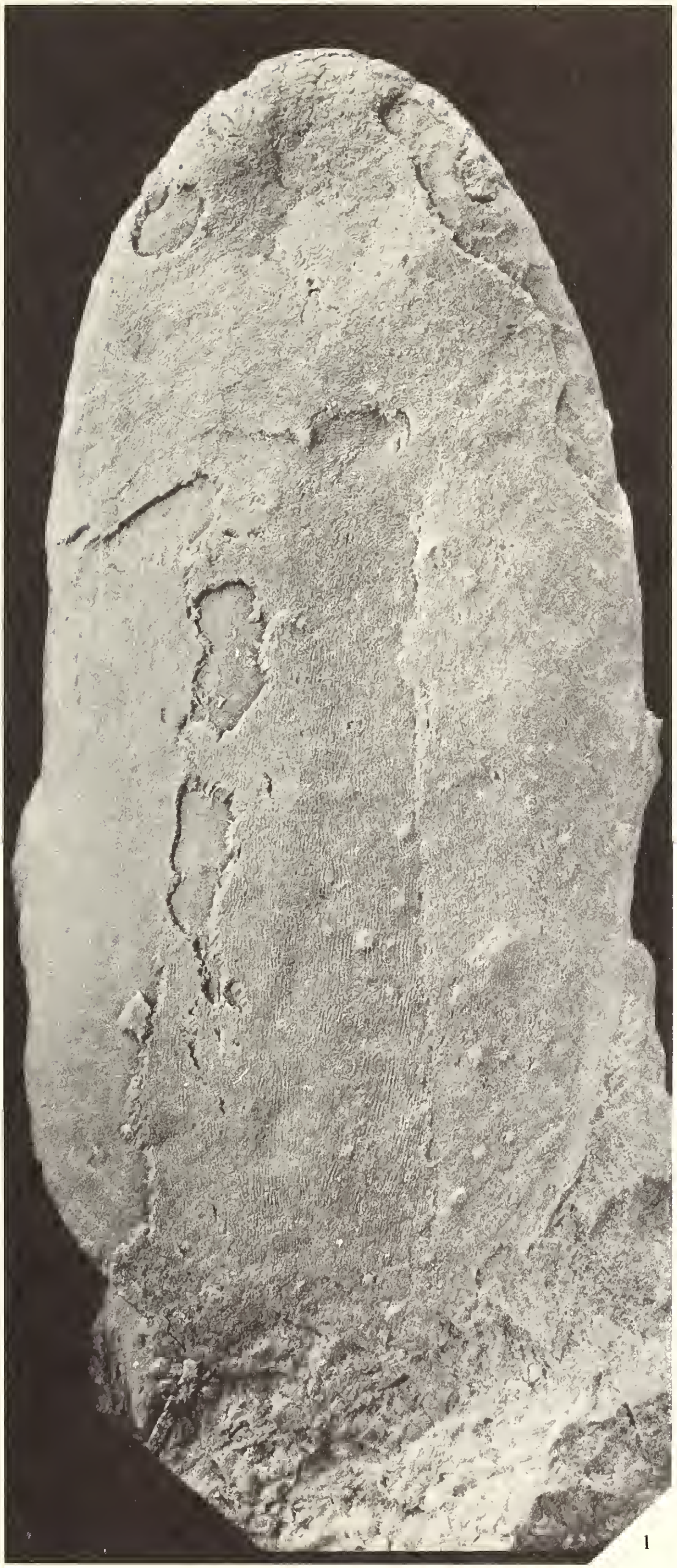
EXPLANATION OF PLATE 114

Corvaspis arctica sp. nov.

Fig. 1. NMC 21600 (holotype), incomplete dorsal shield associated with trunk scales. Magnification approx. ×2.

Fig. 2. NMC 21601, incomplete dorsal shield. Magnification approx. ×1·5.

Fig. 3. NMC 21602, incomplete dorsal shield. Magnification approx. ×1·5.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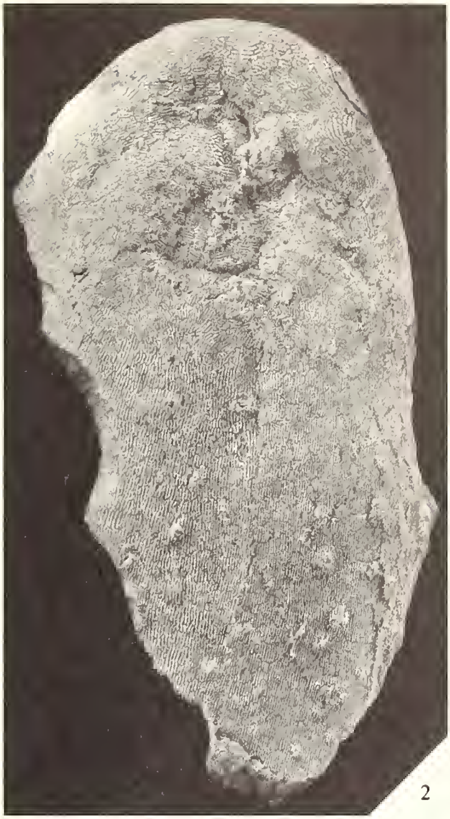
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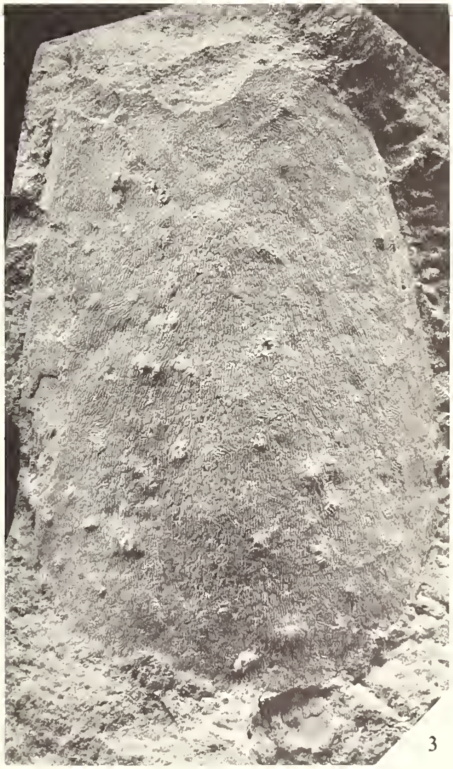
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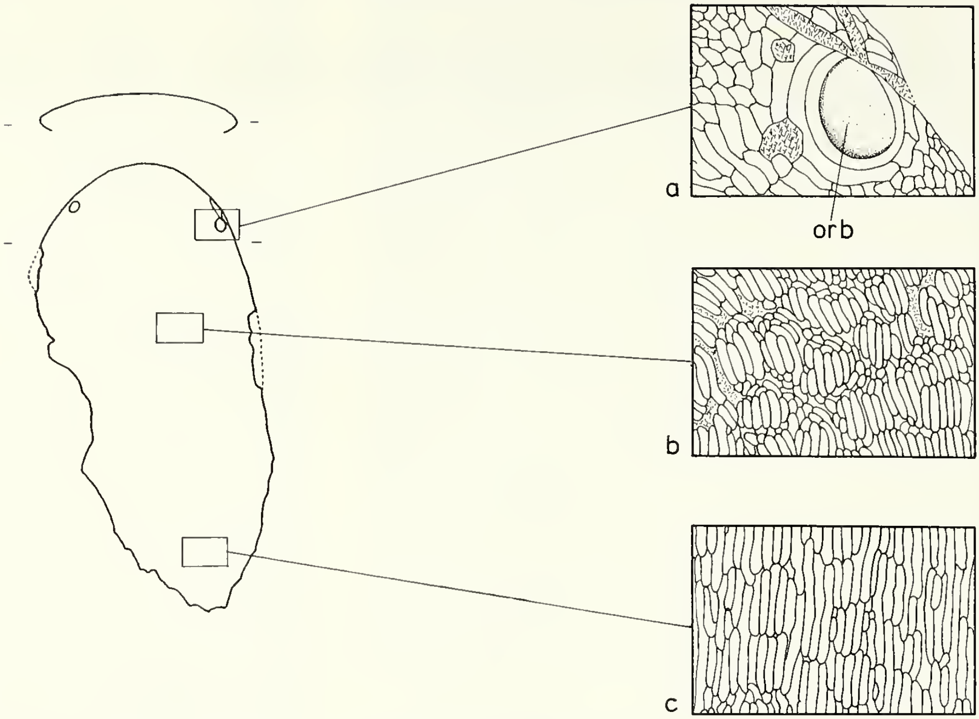
LOEFFLER and DINELEY, *Corvaspis*



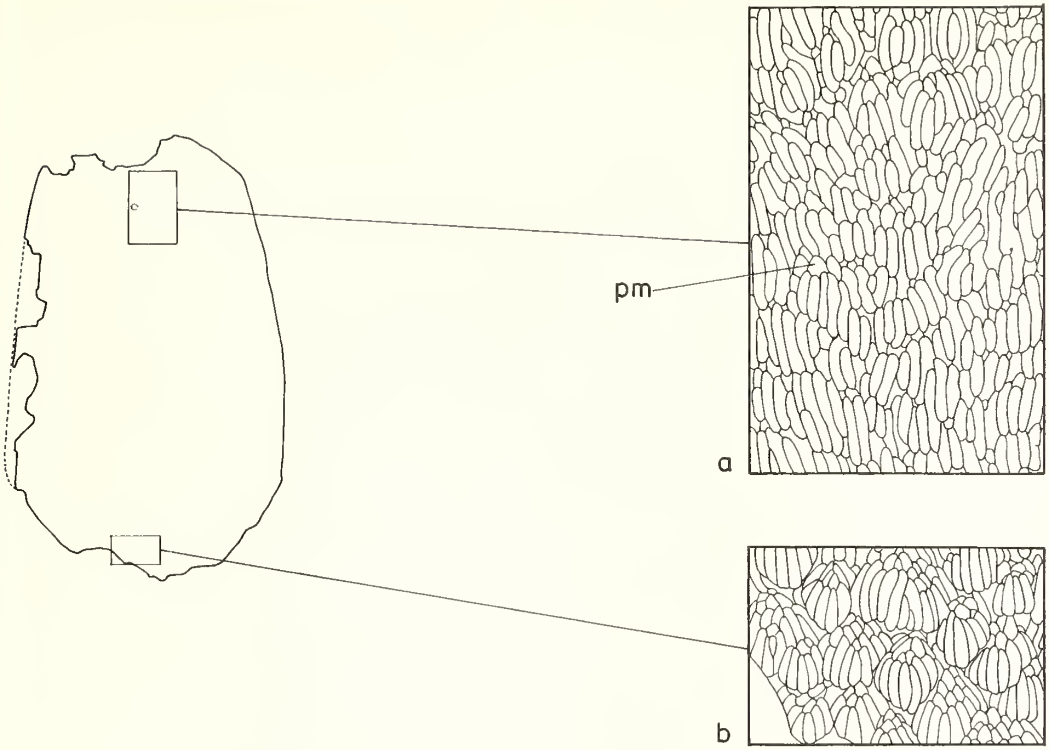
TEXT-FIG. 3. *Corvaspis arctica* sp. nov. Variation in ornamentation of dorsal shield NMC 21601. Plan ×1, detail ×16. orb, orbit.

The orbits, which are best preserved in NMC 21601 (Pl. 114, fig. 2), are encircled by two annular dentine ridges and by numerous short peripheral ridges and tubercles (text-fig. 3*a*). The concentric ornamentation of the orbital region grades into the typical ornamentation of the rostral region without obvious boundaries or sutures.

The pineal region of the holotype is poorly preserved, with broad (0·4 mm) ridges radiating from an abraded macula (text-fig. 2*c*). In NMC 21602, however, the macula is a small tubercle which does not disrupt the surrounding ornamentation (text-fig. 4*a*); it is slightly depressed, suggesting that the pineal region of the shield was particularly thin. The macula is not preserved in NMC 21601.

The ornamentation of the lateral and anterior margins of the dorsal shield is characterized by broader ridges and tubercles than occur elsewhere on the shield. On the rostral margin, the ornamentation is of short ridges and tubercles 0·4–0·8 mm wide (Pl. 114, figs. 1 and 2); in the holotype, these are so irregular and bulbous (text-fig. 2*b*) as to suggest a secondary origin. On the postorbital, lateral margins of the shield, ridges are up to 0·5 mm wide.

The numerous body scales which are associated with the holotype (Pl. 114, fig. 1) are small (1·5–2·0 mm in diameter) and rhomb-shaped. Ornamentation comprises several longitudinal ridges posteriorly, and a variable number of anterior tubercles. The anterior margin of each scale has an unornamented brim approximately 0·2 mm wide.



TEXT-FIG. 4. *Corvaspis arctica* sp. nov. Variation in ornamentation of dorsal shield NMC 21602. Plan × 1, detail × 16. pm, pineal macula.

Remarks. The form of the orbits, and the characteristic ornamentation of short ridges grouped into areas, indicate these specimens as members of the genus *Corvaspis* Woodward. They are distinguished from the three established species (*C. kingi* Woodward, *C. graticulata* Dineley, and *C. karatajuteae* Tarlo) by details of the ornamentation. The width of individual dentine ridges of *C. arctica* sp. nov. is less than that of the other species, and the variety of ornamentation is greater even than in *C. karatajuteae*; although scale-like subdivisions of the shield were described in *C. graticulata* (Dineley 1953), they are not as intricately ornamented as those of *C. arctica*.

MORPHOLOGY OF *CORVASPIS*

C. arctica, the first member of the genus to have been described from other than fragmentary remains, appears to have been a rather streamlined form with a long, narrow, flattish dorsal shield. Despite its similarity in over-all shape to certain of the larger cyathaspidids (such as *Pionaspis* and *Ptomaspis*), the dorsal shield completely encloses the orbits, and extends to cover the ventral faces of the lateral margins of the cephalic region. The armour of the ventral surface of the head, including the oral region, remains unknown; immediately behind the headshield, the trunk appears to have been covered by small imbricating scales.

Previous interpretations of the morphology of *Corvaspis*, based on the remains of *C. kingi*, produced a rather different picture from that outlined above. Dineley (1953) and Tarlo (1960), although differing over details, both visualized *Corvaspis* as a rather large, dorso-ventrally flattened ostracoderm not unlike *Drepanaspis*. Dineley (1953) recognized median, orbital, and ridge plates, postulating that a scaled area or mosaic of small plates surrounded the median disc. Tarlo (1960) with additional British material at his disposal, reinterpreted Dineley's 'ridge plates' as branchial plates and also described a postorbital plate; he inferred, from the pattern of ornamentation, that fields of tesserae (small plates) separated the main plates.

It is not possible to dismiss these accounts as merely being the result of work on fragmentary material. Although similarly shaped and ornamented fragments could be produced by mechanical breakdown of a dorsal shield similar to that of *C. arctica*, such a simple explanation does not appear to be the case. While some of the 'plates' described by Dineley (1953) and Tarlo (1960) could be fragments of larger plates, others show distinctive differences in histology and ornamentation at their margins (Dineley 1953, p. 177, fig. 16), which can consequently only be assumed to have been natural edges. If examples of this were confined to median plates, it might be possible to conclude that they were ventral plates, which are otherwise unknown. Tuberculated or spongy margins are, however, present on many of the asymmetrical plates, including the orbital and the postorbital plates (Tarlo 1960, pl. 37, figs. 2, 4, 7). Thus, although the over-all shape of the carapace may have been similar to that of *C. arctica*, the dorsal armour of *C. kingi* (and possibly also of the other two established species) was apparently divided into plates and tesserae.

Stratigraphic evidence suggests that subdivision of the dorsal armour into plates and tesserae was a late development within the genus; it may have been an adaptation to permit continued growth of the shield. If this was the case, the marginal spongy tissue (Dineley 1953) may have been the zone of active growth, the tuberculated borders marking the increased area. Such growth may account for the irregular shape of the plates, and for the 'incorporated tesserae' which were described by Tarlo (1960).

AFFINITIES OF *CORVASPIS*

When Woodward (1934) first described *C. kingi*, he regarded it as a cyathaspidid. Dineley (1953), however, describing additional British material, considered the enclosed orbits to justify establishing the family Corvaspididae. Stensiö (1958) subsequently suggested that it should be raised to the rank of an order, the Corvaspida. From work on new material from Britain, Tarlo (1960) concluded that *Corvaspis* was sufficiently close to *Drepanaspis* to be placed with it in the family Psammosteidae. In a subsequent revision of the psammosteids, Tarlo (1962, 1964, 1965) referred *Corvaspis* to the order Psammosteiformes, placing the Corvaspididae within the suborder Tesseraspidida. He suggested (1960, 1962, 1964, 1965) that *Cardipeltis* had been derived from the primitive Psammosteiformes (such as *Tesseraspis* and *Kallostrakon*) via *Corvaspis*. The relationship between these forms was based on Tarlo's interpretation of the ornamentation; the lineage was supposed to show progressive stages in the elimination of tesserae.

Following Thorsteinsson and Tozer's report (in Fortier *et al.* 1963) of a cyathaspidid comparing favourably with *Corvaspis*, both Obruchev (1964, 1967) and Halstead (1973) grouped *Corvaspis* with the cyathaspidids. Obruchev (1964) placed the Corvaspididae within the order Cyathaspidiformes, giving it equal status with the Tolypaspididae, Cyathaspididae, Poraspididae, Anglaspididae, and Ctenaspididae. Halstead (1973) provided a similar grouping, but accommodated *Anglaspis* within the Poraspididae, and proposed an evolutionary scheme whereby the cyathaspids and pteraspids were independently derived from tesselated ancestors. Within the cyathaspid lineage, *Corvaspis* was supposed to have been derived from *Kallostrakon* and to have given rise to *Cardipeltis* as well as to the cyathaspids.

C. arctica is closest in over-all appearance to some of the larger cyathaspidids such as *Pionaspis* and *Ptomaspis*, but differs in having enclosed orbits and a ventro-lateral lamina. It particularly resembles *Ptomaspis* in its ornamentation, showing a gradation from short dentine ridges anteriorly to scale-like areas posteriorly. Although Halstead (1973) proposed that *Corvaspis* was derived from *Kallostrakon* and gave rise to the cyathaspids, a shield like that of *C. arctica* could equally well have originated from a primitive, *Ptomaspis*-like, cyathaspidid shield by fusion of the suborbital and also possibly the branchial plate to the lateral margins of the dorsal shield. In view of the morphology of *C. arctica*, the derivation of *Cardipeltis* from *Corvaspis* is also open to question. *Cardipeltis* was shown by Denison (1966) to have been a broad, flat heterostracan with a short tail, a terminal mouth, and dorsal branchial openings which notched a median dorsal disc; small plates cover the rostrum and also form the ventral armour. The only features common to *Corvaspis arctica* and *Cardipeltis* are the short dentine ridges which comprise the ornamentation.

It remains to be shown whether the subdivision of the armour in *Corvaspis kingi* was an important evolutionary step towards the development of tesserate forms, or whether it is an example of the ease with which the shield could be 'mobilized' to permit continued growth.

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MICRO-ORNAMENTATION OF SOME SPIRIFERIDE BRACHIOPODS

by HOWARD BRUNTON

ABSTRACT. The use of the term microspine by Balinski (1975) for a variety of structures on several taxa of spiriferides is discussed and, in part, rejected. Balinski described two distinct structures; true microspines and a papillose ornamentation resulting from external shell erosion. Evidence for a microspinose ornamentation on species of *Crurithyris* is presented together with models distinguishing the growth of spines in spiriferides from that in productaceans.

BALINSKI (1975) described the changes in micro-ornamentation of some Devonian ambocoeliids during progressive stages of weathering. He demonstrated that the original external fine ribbing on *Ilmenia* specimens from the Holy Cross Mountains of Poland was removed by weathering and led to the exposure of a 'microspinous' ornamentation. In terms of shell structure this process involved the progressive loss of the primary shell layer, within which the ribbing was principally developed, and the exposure of externally forwardly projecting 'microspines' aligned radially along the original intercostellate spaces. These 'microspines' are described as being 'coarsely crystalline' and 'generally devoid of a distinct trace of [a] central canal'. Balinski described similar structures in other Givetian ambocoeliids and argued a case for interpreting them as having developed like the true microspines of other spiriferides such as *Nucleospira*, i.e. from mantle epithelium which, during ontogeny of the individual, retracted and sealed the spine cavity by shell deposition. Balinski's contention is, however, that his 'microspines' differ from true microspines in that the former never protruded from the original external surface of the non-weathered specimen. From this standpoint he discussed the dangers in using microspinous ornamentation as taxonomic criteria and suggested that some taxa may be falsely based as a result of ill-preserved material. In addition he suggested that most species of *Crurithyris*, normally described as being microspinous, only developed the type of ornamentation he described for *Ilmenia* by secondary weathering or erosion.

My view is that Balinski's warning of caution in the use of poorly preserved or eroded material is valid and doubtless his explanation of the variable ornamentation of *I. hians* (Buch) is correct. I am not confident that his interpretation of his 'microspines' on this and related species is correct and I am sure that he is incorrect in saying that no *Crurithyris* species ever had a true external ornamentation of a microspinous nature. His use of the term 'microspine' is confusing for a structure distinctive from the true microspines of other spiriferides, such as *Nucleospira*, *Crytina*, or *Spiriferellina* (Pl. 115, figs. 1–7), and I prefer to use here the term papillose for ornamentation protruding from the surface as a result of erosion such as described by Balinski for *I. hians*.

My confidence in asserting the primary nature of an external ornamentation, which I call truly microspinous, on some species of *Crurithyris*, arises from a study of very

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finely silicified Viséan specimens from Co. Fermanagh, Ireland. These specimens belong to *C. urei* (Fleming), the type species of *Crurithyris* George, and are abundant in the silicified faunas collected. In his description of *Crurithyris*, George (1931) detailed the spinose ornamentation of three species, including *C. urei*, and pointed out that there appeared to be two series of spines of distinctly different sizes. My illustration (Pl. 115, fig. 2) shows the broken bases of two distinct sets of microspines on the ventral valve of *C. urei*, as well as the clearly developed lamellose growth-lines towards the anterior margin. I do not believe that this combination of ornaments, spines, and lamellae could have resulted from surface erosion of the shell and believe, therefore, that it is primary. The larger set of spines occurs in a roughly quincuncial arrangement and both must have grown rapidly at the valve margins, in a manner like that described by MacKinnon (1974) for *Spinatrypa* and by Dagis (1974), upon whose illustrations text-fig. 1 is based.

A truly spinose ornamentation, such as that illustrated here and well known on genera such as *Spiriferina*, occurs commonly on sufficiently well-preserved specimens of many taxa of the spiriferida. On the whole these spines differ from the cylindrical spines of the Productidina and Chonetacea in that those of the Spiriferida developed from a fold in the mantle edge whose borders continued to secrete shell material. Such growth led to the development of continually hollow spines, even after mantle retraction, and their cavities were sealed internally by the continued deposition of secondary shell. By contrast the productidine spine developed from a generative bud of mantle epithelium which, while growing away from the external surface, secreted a cylinder of shell material around itself. Some of these spines remained tissue filled until the death of the specimen while others ‘died’ soon after formation as a result of retraction of the epithelial evagination and the plugging of the cavity by shell material during the retraction process.

Unfortunately, since my evidence for spines comes from silicified material I am unable to study the shell structures associated with this ornamentation. However, it seems fairly clear from literature (MacKinnon 1974; Dagis 1974) that endopunctate spiriferinaceans, such as *Spiriferina* and *Labella*, have spines involving the secondary shell layer (and so these spines ‘lived’ longer) while most other microspines, such as those of *Crurithyris*, developed only within the primary layer.

EXPLANATION OF PLATE 115

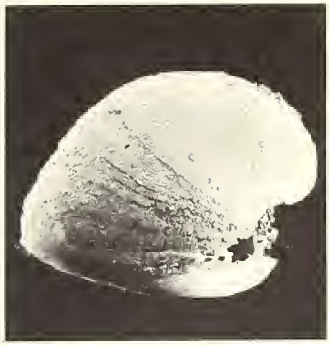
Scanning electron micrographs of three species of spinose Spiriferida, preserved as silica replicas, from the Viséan of Co. Fermanagh, Ireland. The specimens were collected by the author and are housed in the British Museum (Nat. Hist), London.

Figs. 1–2. *Crurithyris urei* (Fleming). 1, complete shell, dorsal valve to the bottom, with spines preserved anteriorly. × 15. BB 61624. 2, detail of antero-median region of the ventral valve showing the two different sizes of microspines. × 75.

Figs. 3–4. *Nucleospira* sp. 3, the posterior half of a ventral valve. × 50. 4, detail from the above picture in which the original hollow centres of the spines can be seen (arrowed). × 150. BB 61625.

Figs. 5–6. *Spiriferellina insculpta* (Phillips). 5, postero-lateral region of the ventral valve showing the bases of several spines, normally associated with rib crests. The umbo is to the right. × 50. 6, detail of two spines from the above specimen which show signs of the original cavities. × 500. BB 61626.

Fig. 7. *Cyrtina* sp. Part of the mid-region of a ventral valve looking towards the commissure. × 50. BB 61627.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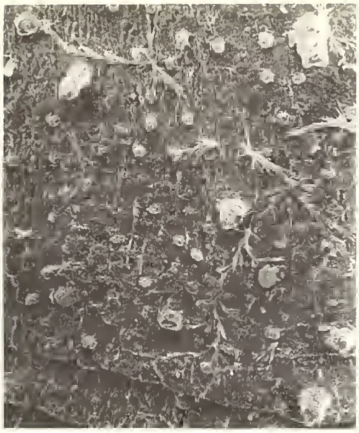
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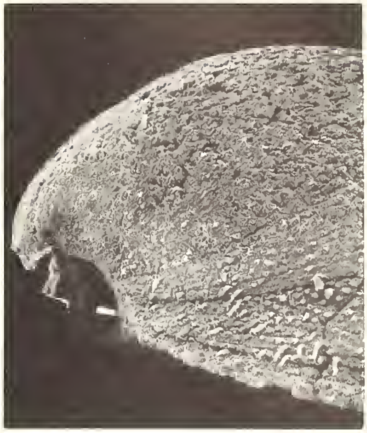
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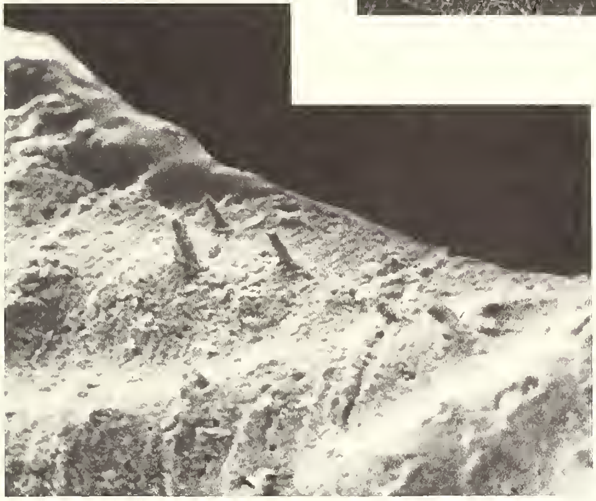
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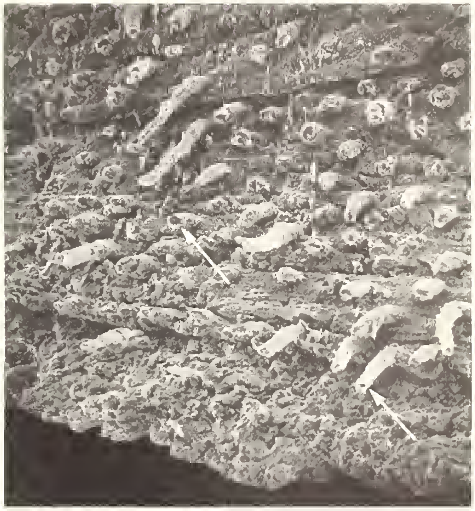
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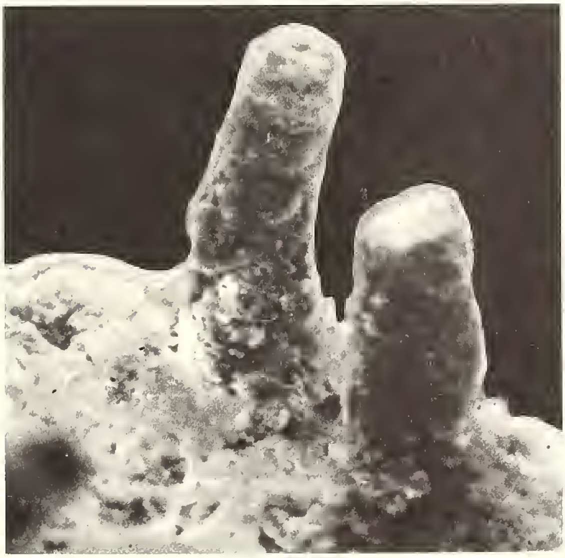
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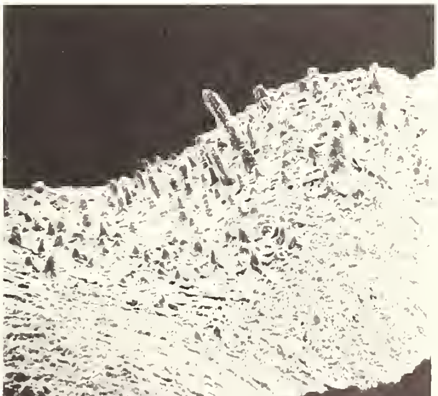
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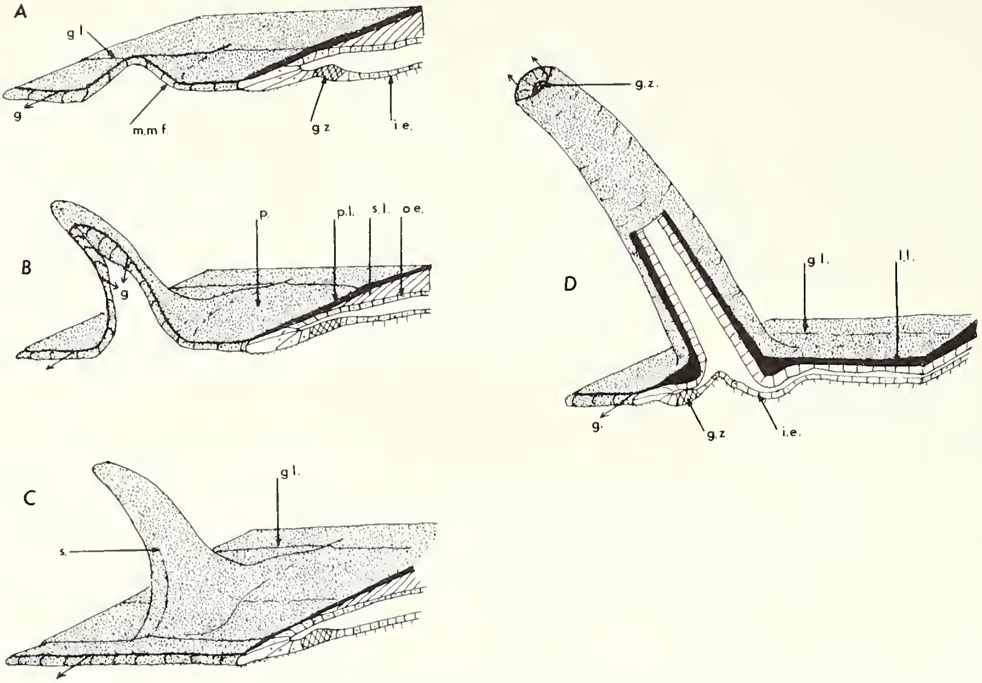
BRUNTON, spiriferide micro-ornamentation



TEXT-FIG. 1. Stylized illustrations showing the development of a spine in a spiriferide (A–C) and a productidine (D). In A the mantle edge started to fold up after the last growth halt (g.l.). In B the forward and outward growth of the mantle fold, and the shell it secreted, has ceased and the mantle edges draw back towards the original valve margin. Mantle edge thickening probably sealed the shell in the spine positions when the valves were closed. In C the spine is complete. The mantle has returned to its normal position and shell has closed the anterior face of the spine. In D the isolated generative zone at the spine tip may continue to proliferate and secrete shell, increasing the spine length, after it has been left well behind the valve margin. Mantle, covered by periostracum, seals the distal end of the spine and inner epithelium the internal opening to the spine. g, growth direction of shell at the valve margin; g.l. growth line, indicating a pause in growth; g.z., generative zone of mantle epithelium; i.e., inner epithelium; l.l., laminar shell layers; m.m.f., mantle margin, folded in this region at the start of development of a spine; o.e., outer epithelium; p., periostracum (dotted) extending over the shell from the generative zone; p.l., primary layer of shell; s., suture line on front face of spine; s.l., secondary layer of shell.

While Balinski thought that his ‘microspines’ on ambocoeliids were secondary structures he nevertheless thought they developed and functioned like true microspines in other spiriferides. Thus although I think him incorrect in extending his *Ilmenia* observations to all other ambocoeliids I think he is generally correct in saying that the structures he saw and illustrated on specimens of *Ambothyris*, *Nucleospira*, and *Proreticularia* are microspines. In addition the different structures he illustrated on eroded *Ilmenia* and *Crurithyris* species should not be termed ‘microspines’ as they are probably quite unrelated to spines (in the normal sense of a protuberance from the surface having considerably greater length than breadth), but are more similar to the papillae seen in the primary shell layer of some terebratellaceans. The terms papillae and spine are general and descriptive but distinctive. The former is ill-defined in the *Treatise* (1965) and should include any conical or nipple-shaped protuberance on inner or outer surfaces, such as are illustrated by Balinski on *Ilmenia* (1975, pl. 33, figs. 2, 5).

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AN OCCURRENCE OF THE TETHYAN AMMONITE *MENEGHINICERAS* IN THE UPPER LIAS OF THE YORKSHIRE COAST

by M. K. HOWARTH

ABSTRACT. A single specimen of *Meneghiniceras lariense* (Meneghini) found in the *Semicelatum* Subzone, *Tenuicostatum* Zone, of the Upper Lias of the north Yorkshire coast, is the only example of the genus found north of the Alps or outside the Tethyan area, and is stratigraphically the youngest occurrence of the genus.

IN 1974 Professor Dr. Ulrich Lehmann of the Geological-Palaeontological Institute of Hamburg University found a specimen of *Meneghiniceras lariense* (Meneghini) in bed 31 of the outcrop of the Grey Shales on the foreshore at Hawsker Bottoms, near Whitby, Yorkshire (grid ref. NZ 948078). This bed is at about the middle of the *Semicelatum* Subzone, the top subzone of the *Tenuicostatum* Zone of the Upper Lias (Howarth 1973, pp. 240-244). Professor Lehmann most kindly presented the ammonite to the collections of the British Museum (Natural History) (reg. no. C. 79625), and has entrusted its description to me. It is worthy of description because *Meneghiniceras* is a typical 'Tethyan ammonite' and this is the first discovery of a specimen outside Tethys. The discovery is also remarkable because of the intensive collecting done in the coastal exposures of the Yorkshire Lias by myself and many others, yet no example of *Meneghiniceras*, nor any other Tethyan ammonite, has ever been found (or recognized) before. Chance discoveries of single specimens like this at large distances from their normal provinces, demonstrate either the wide dispersal of ammonites that can occur after death, or the wide movements made by isolated individuals during life, or the incompleteness of the fossil record where only a very small proportion of a population became preserved as fossils. There is no evidence in this case as to which of these possibilities is the most probable.

Family JURAPHYLLITIDAE Arkell, 1950
Genus MENEGHINICERAS Hyatt, 1900

Type species. Ammonites (*Phylloceras*) *lariensis* Meneghini, 1874, by original designation.

Meneghiniceras lariense (Meneghini)

1874 *Ammonites* (*Phylloceras*) *lariensis* Meneghini, p. 80, pl. 17, figs. 1, 2.

1895 *Rhacophyllites lariensis* (Meneghini) var. *dorsinodosus* Bonarelli, p. 335 (for Meneghini 1875, pl. 17, fig. 1 only).

1895 *Rhacophyllites lariensis* (Meneghini) var. *bicicolae* Bonarelli, p. 355 (for Meneghini 1875, pl. 17, fig. 3).

1900 *Rhacophyllites lariensis* (Meneghini) var. *costicillata* Fucini, p. 154, pl. 20, fig. 3.

1969 *Meneghiniceras lariense* (Meneghini); Pinna, p. 17, pl. 6, fig. 2 (neotype figured).

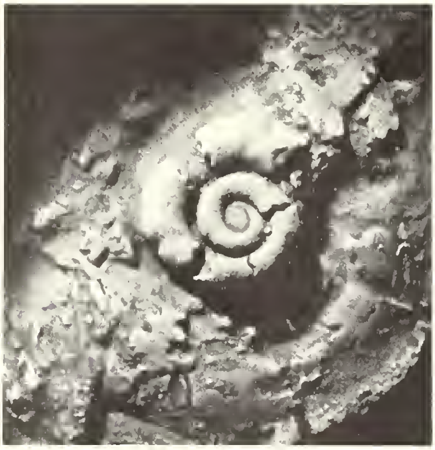
[Palaeontology, Vol. 19, Part 4, 1976, pp. 773-777.]

1969 *Meneghiniceras dorsinodosum* (Bonarelli); Pinna, p. 17, pl. 13, fig. 3 (neotype for *dorsinodosus* figured).

1974 *Meneghiniceras lariense* (Meneghini); Fantini Sestini, pp. 217–219, pl. 19, figs. 1, 2 (see for full synonymy).

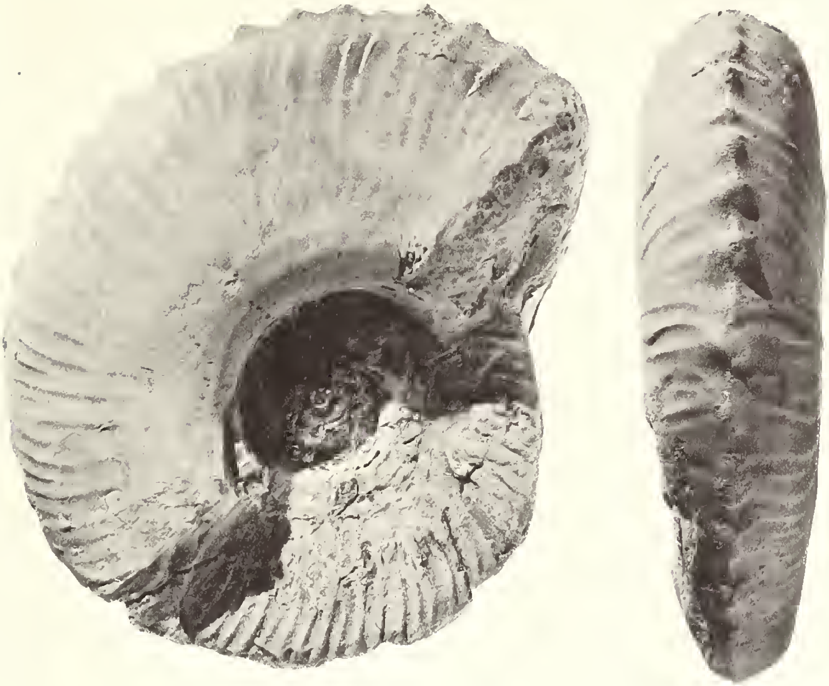
Type. Of the two syntypes figured by Meneghini (1875, pl. 17, figs. 1, 2), one (fig. 1) was used as the type of var. *dorsinodosus* by Bonarelli (1895, p. 335), and the other (fig. 2) was designated lectotype of the species by Fucini (1901, p. 75). This lectotype was destroyed in 1943 (Pinna 1969, p. 8) and a neotype was designated and figured by Pinna (1969, p. 17, pl. 6, fig. 2) as a replacement.

Description. The specimen consists of solid pyritized inner whorls, followed by crushed whorls for the remainder of the phragmocone, then a solid, mainly uncrushed body chamber. The innermost whorls (text-fig. 1) are preserved as a solid internal cast of iron pyrites on the exposed side only, the preserved part not quite reaching the middle of the venter. Some of the septa are preserved and the outline of the protoconch is just visible. The diameter at the mouth of the protoconch is approximately 0·23 mm, and this is followed by $3\frac{1}{8}$ whorls ending at 3·2 mm diameter at the end of the solidly preserved part. The first three whorls are almost completely evolute, with a whorl breadth that appears to exceed the whorl height throughout (i.e. a depressed whorl cross-section), and they have no ornament, except for three oblique constrictions on the last whorl. The suture-lines are at an early stage of development and show three saddles on the side of the whorl, but neither the mid-ventral nor the mid-dorsal parts are clearly seen. These solid inner $3\frac{1}{8}$ whorls are followed by crushed whorls up to $6\frac{5}{8}$ whorls from the protoconch. Whorls from $3\frac{1}{8}$ to $6\frac{1}{4}$ are very poorly preserved, with no ornament or constrictions visible and only small parts of the suture-lines can be seen, some of which have phylloid saddle endings. The whorl from $6\frac{1}{4}$ to $6\frac{5}{8}$ is the smaller half of the outer whorl, and here ornament can be seen to consist of slightly prorsiradiate ribs on the outer half of the side of the whorl, that curve forwards on approaching the venter. The inner half of the whorl side appears to be smooth, but traces of two constrictions cross the whorl. The shape of the middle of the venter is not clearly seen due to crushing, but it appears to be bluntly angled without a differentiated keel and without mid-ventral tubercles. On this and at least the previous whole whorl, the whorls have become much more involute.



TEXT-FIG. 1. Innermost whorls of text-fig. 2, enlarged ×7·5, showing evolute whorls and two constrictions.

The last half whorl is body chamber (text-fig. 2) and the present aperture is probably at or very close to the mouth border. The body chamber is about half involute, with nearly flat whorl sides, an arched venter, a bluntly angled umbilical edge, and a narrow sloping umbilical wall. The smooth inner whorl side and the prorsiradiate ribs on the outer part of the whorl side are now more clearly seen; the venter is bluntly angled at the beginning, then mid-ventral clavate tubercles quickly develop on the final quarter whorl. The ribs are joined in twos or threes to the tubercles and some of them



TEXT-FIG. 2. *Meneghiniceras lariense* (Meneghini), bed 31, Grey Shales, *Semicelatum* Subzone, *Tenuicostatum* Zone, Hawsker Bottoms (NZ 948078), Whitby, Yorkshire. BM C. 79625. Natural size.

bend suddenly backwards just before reaching the tubercles. There are ten ventral tubercles and twenty-three ribs on a length of exactly one-quarter whorl ending two tubercles before the aperture. The last two tubercles appear to be diminishing in size and the venter and umbilical border become excentric, resulting in a slight decrease in whorl height at the aperture, suggesting that it is at or very close to the adult mouth border. If so, the complete ammonite has $7\frac{1}{8}$ whorls from the protoconch, and has an adult body chamber of slightly less than half a whorl in length. Parts of the last suture-line occur on the beginning of the uncrushed final half whorl and triple phylloid endings can be seen to the 1st and 2nd lateral and the two auxiliary saddles outside the umbilical seam. The diameter at the aperture is 93 mm, and the diameter at the final suture-line is 71 mm. Approximate whorl dimensions shortly before the aperture are: diameter 87·0 mm, whorl height 36·7 mm (0·42 of the diameter), whorl breadth 24·7 mm (0·28), width of umbilicus 25·5 mm (0·29).

Remarks. Meneghiniceras is a monospecific genus of the family Juraphyllitidae, characterized by an obtusely angled venter on the outer one or two whorls of the phragmocone, and by a row of mid-ventral tubercles on the adult body chamber.

The most closely related genus is *Harpophylloceras*, which differs in having an obtuse ventral keel up to the end of the adult body chamber. Both genera, like other members of the Juraphyllitidae, have larger umbilici (usually 15–30% of the diameter) than contemporaneous members of the family Phylloceratidae. The full synonymy of the species *M. lariense* (Meneghini) was given by Fantini Sestini (1974, p. 217), and her complete list of figured specimens is not repeated here. Instead, only those references concerned with the taxonomic names and their type specimens are included in the synonymy above, and it will be seen that three varietal names have been proposed. They are for three Italian specimens that have more numerous rounded ventral tubercles (var. *dorsinodosus*) or more ribs (var. *bicicolae*) than the typical form, or (var. *costicillata*) are possibly transitional to *H. eximium*. I agree with Fantini Sestini (1974, p. 219) that these differences are not more than individual variation between specimens, reflecting the type of preservation and the presence or absence of shell in some cases, and there is no need to raise any of them to specific rank, as was done by Pinna (1969, p. 17, pl. 3, fig. 13) for *dorsinodosum*. In fact the considerable number of Italian specimens that have been figured show that the density of the ribbing varies between fine and moderately coarse, and the ventral tubercles are variously small or moderate in size and may be rounded or clavate.

The Yorkshire specimen has slightly less than half a whorl of adult body chamber, and it seems probable that this is the full extent of the adult body chamber in this species. The ventral tubercles appear to be a feature of the adult body chamber only, and the size range of complete adults is about 50–105 mm. The largest known specimen is from Taormina, Sicily, and was figured by Fucini (1923, p. 104, pl. 7, fig. 4); it is 105 mm diameter at the mouth border and has very long pointed mid-ventral tubercles, whose length probably shows the shape of the outer surface of the shell. The Yorkshire specimen is 93 mm diameter and is one of the larger specimens in the size range; its body chamber is an internal mould and its smaller rounded tubercles show the form of the inside surface of the shell. Rounded tubercles and the fairly widely spaced ribs is a combination of characters that cuts across the 'varieties' discussed above, and is further evidence that they are no more than differences between individuals.

The earliest whorls are seen well in the Yorkshire specimen and they have not been described before in *Meneghiniceras*. The first three whorls after the protoconch are depressed and almost completely evolute, then rapidly become more involute on the fourth and fifth whorls, while constrictions appear on the third whorl. In these characters they are generally similar to the early whorls of *Tragophylloceras* (another genus of the Juraphyllitidae) described by Spath (1914). The suture-lines have triple phylloid endings and agree with other Juraphyllitidae.

Other British Juraphyllitidae have been described by Howarth and Donovan (1964) and this Yorkshire *Meneghiniceras* is a new record for Britain, or for any part of Europe north of the Alps. The known geographical distribution of *Meneghiniceras* is Italy and Sicily (the main area with probably more than 100 specimens known), Switzerland, Austria, Czechoslovakia, Hungary, and southern Spain (Andalusia), the records from which can be found in Fantini Sestini's (1974) description. A hitherto unrecorded occurrence is in the Middle Lias (i.e. Domerian) of Algeria, represented by specimen C. 52918 (British Museum (Nat. Hist.) collection) from between Tola

Guiolet and Lac Goulmine in the Djurdjura mountain range. This specimen is a half whorl fragment, half phragmocone, half adult body chamber, of about 68 mm maximum diameter, and agrees in all respects with the Italian fauna. All these specimens come from the *Margaritatus* and *Spinatum* Zones, i.e. the Domerian, though the stratigraphy in Italy is not always so accurate, and some examples may be from the *Tenuicostatum* Zone at the base of the Toarcian. In Hungary, Géczy's (1972, pp. 55–58) records show that specimens first appear in the *Davoei* Zone at the top of the Carixian (Lower Pliensbachian). The Yorkshire specimen is from the *Semicelatum* Subzone, the top subzone of the *Tenuicostatum* Zone, and is the youngest occurrence of *Meneghiniceras* recorded so far.

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THE PALAEONTOLOGICAL ASSOCIATION

Annual Report of the Council for 1975

MEMBERSHIP AND SUBSCRIPTIONS. Membership of the Association totalled a record 1,523 on 31 December 1975, an increase of 92 since 31 December 1974. There were 902 Ordinary Members, an increase of 62; 234 Student Members, an increase of 36; and 387 Institutional Members, a decrease of 6. Three hundred and eighty institutions subscribed to *Palaeontology* through Blackwell's agency, maintaining the record level of 1974. In addition, 147 individual and 98 Institutional Members subscribed to *Special Papers in Palaeontology* for the year, an increase of 25 and decrease of 5 respectively since 31 December 1974. One hundred and forty-four Institutions again subscribed via Blackwell's agency. Total subscriptions to the series therefore reached a new high level. Sales of back parts of *Palaeontology* to members via the Membership Treasurer increased from 19 transactions in 1974 to 21 in 1975, maintaining the significant increase from 2 transactions in 1973. Similar sales of *Special Papers* also increased, from 90 transactions in 1974 to 110 in 1975. Administratively, these welcome increases in membership and sales involve an increase in the number of changes to mailing lists and of dispatch authorizations. The Association and Press therefore streamlined procedures during the year to improve speed and efficiency of operation.

FINANCE. During 1975 the Association published Volume 18 of *Palaeontology* at an estimated cost of £21,907, and *Special Papers 15* and *16* which cost £4,420. The total printing bill of £26,327 is only a little less than in 1974 in spite of a smaller volume of *Palaeontology* and a much smaller total volume in *Special Papers*. Total expenditure was larger than ever at £29,820. The higher figure than last year is accounted for by the increase in the cost of circulars (and most of this arises from higher postal charges) plus our first recorded loss on the sale of offprints. Total income in 1975 was £25,258 which was slightly larger than in the previous year but still left a deficiency against expenditure of £4,562. This would have been worse but for donations from the Smithsonian Institution, the National Museum of Victoria, and Dr. R. G. Bromley towards the cost of individual papers in *Palaeontology*. The Association is most grateful for these gifts. The reserves of the Association now stand at £14,356 which in real terms is the lowest for many years. The increases in subscriptions and sale charges in 1976 will now barely cover the still higher printing costs, and a further increase in subscriptions will be necessary soon.

PUBLICATIONS. Four parts of Volume 18 were published during 1975; they contained 49 papers and 5 short communications consisting of 899 pages and 105 plates. Two *Special Papers* have been published during the year. *Special Paper 15* 'Lower and Middle Devonian Conodonts from the Broken River Embayment, North Queensland, Australia' and *Special Paper 16* 'The Ostracod Fauna from the Santonian Chalk (Upper Cretaceous) of Gingin, Western Australia' were both published in August.

MEETINGS. Four meetings were held during 1975. The Association is indebted to Professor T. S. Westoll, F.R.S. for granting facilities for the meeting at Newcastle, to the local secretary for that meeting, and to the leaders of the field excursions.

a. The *Eighteenth Annual General Meeting* was held in the Lecture Theatre of the Geological Society of London on 5 March 1975. Professor W. G. Chaloner (Birkbeck College, London) delivered the *Eighteenth Annual Address* on 'The Palaeoclimatic Significance of Fossil Plants'.

b. A *Field Demonstration Meeting* was organized by the Carboniferous Group on the 'Carboniferous of the Dublin area' and led by Dr. G. D. Sevastopulo (Trinity College, Dublin). Fifty-one members attended the meeting which was held on 19–21 April 1975.

c. A *Field Demonstration Meeting* on the Eastern Mendips was held on 25–27 April 1975 and was led by Dr. H. S. Torrens and Mr. C. Copp (Keele): 34 members attended.

d. The *Annual Christmas Meeting* was an Open Meeting held at the University of Newcastle upon Tyne at which twenty-seven papers, a film, and twenty-six demonstrations were presented on a wide variety of palaeontological topics. About 130 members attended the sessions on 22–23 December 1975. Three field excursions were organized jointly with the British Sedimentological Research Group on 21 December 1975 and were led by Dr. D. B. Smith (I.G.S., Leeds), Dr. G. A. L. Johnson (Durham), and Dr. J. M. Jones with Dr. D. G. Murchison (Newcastle). The local secretary was Mr. J. H. Powell.

COUNCIL. The following were elected members of Council for 1975–1976 at the A.G.M. on 5 March 1975: *President*: Professor C. H. Holland; *Vice-Presidents*: Dr. W. D. I. Rolfe, Dr. J. D. Hudson; *Treasurer:* Dr. J. M. Hancock; *Membership Treasurer*: Dr. E. P. F. Rose; *Secretary*: Dr. C. T. Scrutton; *Editors*: Dr. L. R. M. Cocks, Dr. C. P. Hughes, Professor J. W. Murray, Dr. C. B. Cox; *Other members*: Dr. D. D. Bayliss, Dr. M. C. Boulter (Circular Reporter), Dr. C. H. C. Brunton, Dr. J. C. W. Cope, Dr. G. P. Larwood, Dr. C. R. C. Paul, Dr. J. E. Pollard, Dr. R. E. H. Reid, Dr. R. B. Rickards, Dr. A. W. A. Rushton, Dr. E. B. Selwood, Professor D. Skevington, Dr. P. Toghill, Dr. P. Wallace.

CIRCULARS. Four Circulars, nos. 79–82, were distributed to Ordinary and Student Members and over a hundred Institutional Members on demand during 1975. During the year address labels for the Circulars were computerized to reduce the work load on the production team in Newcastle.

COUNCIL ACTIVITIES. Major innovations in 1975 have arisen as a result of recommendations of the Planning Committee set up last year. Council has authorized the establishment of a *Conservation Fund* from which grants will be made towards the preservation of sites of palaeontological interest. A sum of £100 per annum has been set aside for this fund in the first instance. Grants of £100 per year for 1975 and 1976 have been made to Shropshire Conservation Trust towards the purchase and maintenance of Comley and Meadowtown Quarries. In addition, Council has agreed to make limited financial assistance available to help the establishment of newsletters of palaeontological interest. Council continues to review suggestions for additional meetings as well as arranging the established programme. Plans are now under way for an International Symposium on the Devonian System to be held in Bristol in September 1978. Opportunities to hold joint meetings with other societies are always welcome. The field excursions organized with the British Sedimentological Research Group in connection with the Open Meeting at Newcastle attracted about 180 participants. Future joint meetings are planned with the Earth Science Education Methods Group of the Geological Society and with the Geological Curators Group. Council has appointed or reappointed representatives on several outside bodies this year; Mr. F. C. Dilley replaces Dr. W. D. I. Rolfe as a Treatise Advisor, Professor C. H. Holland replaces Mr. N. F. Hughes on the British National Committee for Geology, and Dr. C. B. Cox replaces Dr. W. S. McKerrow as our International Palaeontological Association representative. Our thanks are due to Dr. Rolfe, Mr. Hughes, and Dr. McKerrow for their services to the Association in these posts. Professor M. R. House and Professor W. G. Chaloner have been reappointed to the Zoology and Botany Subcommittees respectively of the British National Committee for Biology. Dr. P. Toghill represents the Association on the newly formed Working Party on Geological Conservation. Council has appointed Dr. O. A. Reig (Universidad de Los Andes, Merida, Venezuela) as the Association's first Overseas Representative for South America.

BALANCE SHEET AND ACCOUNTS
FOR THE YEAR ENDING 31 DECEMBER 1975

Balance Sheet as at 31 December 1975

1974 £	LIABILITIES	£ p
	Publications Reserve Account:	
18,913	Balance as per annexed account	13,995·90
300	Royal Society Loan	300·00
505	Adelaide University Loan	505·05
	Amounts received in advance:	
360	Subscriptions for 1976	724·24
14,300	Provision for cost of publication of *Palaeontology*, Volume 18, part 4, as per Income and Expenditure Account	6,000·00
	Provision for printing *Special Papers* as per Income and Expenditure Account:	
8,003	*Special Papers 13* and *14*	—
431	Sundry creditors	64·80
£42,812		£21,589·99

1974 £	ASSETS	£ p	£ p
	Office equipment at cost	136·82	
	Less Depreciation to date	126·82	
25			10·00
	Investments at cost:		
	Agricultural Mortgage Corporation £2,000 9¼% Debenture Stock 1980/1985	1,937·60	
	Bootle Corporation 7¾% Redeemable Stock 1977/1979	1,123·95	
	City of Chester Loan	1,000·00	
	Clyde Port Authority 7½% Bonds 1977	722·12	
	Equities Investment Fund for Charities, 5,270 Units	4,073·07	
	Imperial Group Ltd., £2,000 8% Conv. Unsecured Loan Stock 1985/1990	1,404·85	
	New Court European Trust, 450 25p shares	450·00	
	New Throgmorton Trust Ltd., 10,000 25p Income Shares	1,706·36	
	Throgmorton Trust Ltd., 2,500 Income Shares	982·35	
	£1,000 9% Treasury Stock 1992/1996	991·48	
	£1,000 9% Treasury Stock 1994	955·00	
	£4,000 8% Treasury Stock 2002/2006	2,192·37	
26,219			17,539·15
	Sundry debtors and payments in advance:		
1,161	Authors for offprints	605·31	
	Income Tax refund:		
176	1972 investment income	—	
280	1973 investment income	—	
509	1974 investment income	—	
—	1975 investment income	711·71	
			1,317·02
—	Advance payments for offprints		529·60
	Cash at Bank:		
11,881	Deposit Account	1,045·22	
2,561	Current Account—Sheffield	1,149·00	
			2,194·22
£42,812			£21,589·99

Income and Expenditure Account for the Year Ended 31 December 1975

EXPENDITURE

1974 £		£ p	£ p
	Cost of publication of *Palaeontology*:		
	Volume 18, part 1	5,033·10	
	part 2	5,420·20	
	part 3	5,454·00	
	Provision for part 4	6,000·00	
	Underprovision:		
	Volume 17, part 2	7·00	
	part 3	18·25	
	part 4	566·15	
17,863			22,498·70
	Cost of publication of *Special Papers*:		
	Nos. *15* and *16*	4,419·75	
	Less excess provision for *Special Papers* Nos. *13* and *14*	799·00	
8,003			3,620·75
121	*Special Papers*—Offprints		593·87
	Administrative expenses:		
	Postage and stationery	567·47	
	Audit fee	64·80	
	Duplicating and dispatch of circulars	1,637·34	
	Meeting expenses	502·95	
	Sundries	59·98	
	Membership Treasurer—Honorarium	125·00	
	Membership of Societies	23·00	
2,174			2,980·54
	Grant Shropshire Conservation Trust:		
—	Miscellaneous expenses *less* receipts		100·00
100	Loan interest		10·69
20	Depreciation of equipment		15·00
£28,281			£29,819·55
4,395	Excess of expenditure over income		4,916·93
18,913	Balance as per balance sheet		13,995·90
£23,308			£18,912·83

INCOME

1974 £		£ p	£ p
8,760	Subscriptions for 1975	9,090·06	
670	Subscriptions for 1974	335·25	
			9,425·31
	Sales of publications:		
	Gross income	5,929·42	
	Offprints profit	—	
5,091			5,929·42
128	Profit on sale of investments		266·97
	Investment income (gross):		
	Agric. Mort. Corp. 9¼% Deb. Stock 1980/1985	185·00	
	Bank deposit account	294·08	
	City of Chester Loan	102·87	
	Equities Investment Fund for Charities	463·76	
	Foreign and Colonial Investment Trust	18·04	
	Simon Engineering Co. Ltd.	70·85	
	Knowsley U.D.C. Mort. Loan at 11%	110·00	
	Throgmorton Trust Ltd.	134·36	
	New Throgmorton Trust Ltd.	253·00	
	9% Treasury Stock 1994	90·00	
	Wagon Finance Corporation Ltd.	133·80	
	9% Treasury Stock 1992/1996	90·00	
	New Court European Trust Ltd.	12·76	
	Preston Borough Council 13½% Loan	225·99	
	Imperial Group Ltd. 8% Conv. Unsec. Loan 1985/1990	160·00	
	Imperial Chemical Industries Ltd.	54·59	
	Clyde Port Authority 7½% Bond 1977	112·50	
	Treasury 8% Loan Stock 2002/2006	320·00	
	Bootle Corporation 7¾% Red. Stock 1977/1979	116·26	
		2,947·86	
	Less Holding charges, etc.	14·74	
2,854			2,933·12
316	Special donations		403·73
	Special Papers:		
	Sales	4,384·02	
	Donations	1,560·05	
5,985			5,944·07
82	Miscellaneous receipts *less* expenses		—
	Excess of expenditure over income for the year transferred		
4,395	to Publications Reserve Account		4,916·93
£28,281			£29,819·55
23,308	Balance at 31 December 1974		18,912·83
£23,308			£18,912·83

J. M. Hancock *Honorary Treasurer*

Report of the Auditors to the Members of The Palaeontological Association. We have examined the above balance sheet and annexed income and expenditure account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1975 and of its income for the year ended on that date.

Thornton Baker & Co.
Chartered Accountants, Auditors

Sheffield, 4 March 1976

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